TWO DECADES OF VEGETATION CHANGE ACROSS TUSSOCK GRASSLANDS IN NEW ZEALAND'S SOUTH ISLAND

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Abstract

New Zealand's South Island tussock grasslands have been highly modified by human activities, including burning, grazing and introductions of exotic plants for pastoralism. Studies suggest that tussock grasslands are degraded, in that native species have declined, and exotic species have increased in both diversity and abundance. These trends are primarily thought to be related to the impacts of grazing and subsequent grazing removal. Few studies have assessed long-term changes that have occurred in tussock grasslands, and those that have are generally limited to one particular location.

This thesis aimed to investigate temporal changes in community structure in tussock grasslands, and relate these changes to environmental variables and land tenure. Data were used from 90 permanently-marked vegetation transects, which were set up on 19 geographically widespread properties in areas of tussock grassland across Canterbury and Otago in the South Island of New Zealand. The transects were on land in both conservation and pastoral tenure. Each transect was 100 m, and consisted of 50 0.25 m^2 quadrats. The transects were measured between 1982 and 1986 (first measurement), were re-measured between 1993 and 1999 (second measurement) and again between 2005 and 2006 (third measurement).

A total of 347 vascular species were observed over the 90 transects and three measurement times. Species richness declined between the first and second measurements (first time interval), and increased between the second and third measurements (second time interval), at both the small (quadrat) and large (transect) scales. Both native and exotic species declined in mean quadrat species richness during the first time interval, and then increased during the

second time interval. Changes in mean quadrat species richness were similar on transects in both conservation and pastoral tenure.

Multivariate analysis of species' occurrences in quadrats identified a long gradient in species composition for these 90 transects. Four key plant communities were identifed along this gradient and differed in their mean elevation: (1) Highly-modified pastoral community, (2) Short-tussock grassland community, (3) Tall-tussock grassland community, (4) Alpine mat-forming species community.

A detailed investigation into temporal changes that occurred on 53 transects that occurred in short- and tall-tussock grassland communities showed that changes in species composition were not consistent over time. Transects on different properties changed in species composition by different amounts. Specifically, in ordination space, transects on two properties changed in composition significantly more than transects on one other property. The property that a transect was on also affected the way that it changed in composition, i.e. native species were more likely to have increased on transects on some properties.

Transects in conservation tenure did not change in species richness or composition differently from those in pastoral tenure. Considering that many native plants in tussock grasslands are relatively slow-growing, and that these areas have been grazed and burned for more than a century, we may expect it to be some time before we can detect differences in vegetation dynamics on conservation land from that on pastoral land.

The changes in the community structure of these tussock grasslands were related to a combination of environmental factors, such as soil chemistry, climate, and management factors. This study has allowed greater understanding of vegetation change in tussock grasslands, and demonstrates the importance of long-term ecological monitoring in making reliable and accurate predictions about landscape-scale changes in tussock grassland community structure.

Keywords: Vegetation change; plant species richness; plant species composition; management; tenure; *Hieracium* spp.; *Chionochloa* spp.; tussock grasslands; vegetation monitoring

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Chapter 1: Introduction

New Zealand's South Island tussock grasslands have been highly modified by human activities, including burning, grazing and introductions of exotic plants for pastoralism. This has led to studies of vegetation change in tussock grasslands becoming a key area of interest for scientists, farmers and conservationists.

The aim of this study was to investigate changes that have occurred in plant community structure in geographically widespread locations of tussock grasslands over 24 years, and relate these changes to environmental variables and land tenure. This will give us a deeper understanding of the long-term patterns and changes in community structure in tussock grasslands.

1. New Zealand's South Island tussock grasslands

The dynamics of change in community structure in tussock grasslands are likely to be largely unpredictable, because tussock grasslands have become widespread due to relatively recent human activities. New Zealand was predominantly forested before the arrival of humans; grasslands are thought to have been mostly restricted to above treeline. Mixtures of grassland and shrubland were also common, especially in areas prone to disturbance such as river terraces (McGlone 1989, Mark 1993). Widespread clearing and burning of forests began with the settlement of Polynesian people approximately 1000 years ago (McGlone 1989). This deforestation led to grasslands becoming widespread so that by the time Europeans began settling New Zealand approximately 800 years later, tussock grasslands covered one-third of New Zealand (Mark 1993). Short-tussock grasslands dominated by *Festuca novae-zelandiae* (fescue tussock: Poaceae) and *Poa cita* (silver tussock: Poaceae) were widespread at low elevations, while tall-tussock grasslands dominated by *Chionochloa* species (snow tussock: Poaceae) were more common at high elevations (Mark 1993).

New Zealand's flora evolved in the absence of frequent fires or large mammalian herbivores, both of which can be seen as consumers of vegetation which influence plant community structure (Bond and Keeley 2005). The introduction of both of these factors during Polynesian and European settlement periods, and the loss of indigenous avian herbivores, had dramatic impacts on plant community structure in tussock grasslands (Mark 1965a, Calder et al. 1992,

Yeates and Lee 1997). Burning frequency increased during European settlement to maintain grasslands for grazing, primarily by merino sheep (*Ovis* spp.) (Zotov 1938, Buchanan 1968, Mark 1993). Burning continues to be used as a management tool, albeit less frequently than in the past, to encourage growth of palatable species and to clear areas for oversowing seed of exotic pasture species (O'Connor 1981, Espie and Barratt 2006). This type of management can have large impacts on changes in plant community structure, through directly altering species composition (Calder et al. 1992, Yeates and Lee 1997).

Palatable exotic plant species were introduced to tussock grasslands to increase stocking rates of domestic stock, and to prevent extensive soil erosion that was occurring as a result of overgrazing (O'Connor 2003). Although many exotic species were introduced deliberately, some were accidental as a result of seed contamination (Douglas 1974). For example, in 1869 one bag of seed imported from Britain contained 21 pasture species, and 37 weed species (Thomson in Douglas 1974). These fast-growing exotic species can outcompete slower-growing natives, which has led to competitive exclusion and declines in native species in localised areas (Lord 1990, Rose et al. 1998, Walker 2000). It has yet to be seen how widespread these changes in community composition are at the landscape scale.

Invasion by exotic species is a key threat to New Zealand's vascular native plants (Dopson et al. 1999). Species in the genus *Hieracium* (hawkweed: Asteraceae) are of particular concern in South Island tussock grasslands because they can dominate intertussock spaces, particularly two geographically widespread species, *H. pilosella* and *H. praeltum*. This alters community structure and vegetation dynamics by excluding the establishment of other species (Treskonova 1991). *H. pilosella* is efficient at sequestering nitrogen from the soil (Scott et al. 2001), which may contribute to its increase in most areas of tussock grasslands since the 1960s, regardless of grazing and environmental conditions (Treskonova 1991, Scott 1993, Jensen et al. 1997, Rose et al. 1998, Rose and Frampton 1999, Duncan et al. 2001). For example, *Hieracium* species have increased over time in Otago (Johnstone et al. 1999), the Mackenzie Country (Treskonova 1991, Meurk et al. 2002) and in Marlborough (Rose et al. 1995, Rose et al. 1998). This invasion by *Hieracium* in many localised areas has caused major concern for maintaining biodiversity in New Zealand's South Island tussock grasslands (Rose et al. 1998). *Hieracium* appears to be continuing to spread throughout tussock grasslands of the New Zealand high country, with no signs of stopping, and few factors limiting its spread (Duncan et al. 1997, Rose et al. 1998).

Tussock grassland plant communities have been severely impacted by rabbits. The presence of patches of exotic species in short-tussock grasslands in the Mackenzie Country have been attributed to the effects of the introduced rabbit (*Oryctolagus cuniculus*) (Connor 1964). A reduction in the rabbit population leads to increased pasture biomass and more pasture species (Thomas 1960, O'Connor 1981, Wills and Beggs 1986, Norbury et al. 2002). Fluctuations in rabbit populations occur regularly. The most recent peak in the rabbit population in the South Island was in the 1980s, which declined just after that with the introduction of rabbit haemorrhagic disease (RCD) in 1997 (Hunter and Scott 1997, Parkes et al. 2002). For example, on Earnscleugh Station in Central Otago in 1994, there were an average of 30-42 rabbits per spotlight kilometre, which was reduced to 3-6 rabbits in 1998 after RCD was introduced (Norbury et al. 2002). These continued fluctuations in rabbit populations are likely to influence changes in tussock grassland plant communities.

Conservation of New Zealand's biodiversity has been identified as a priority by the Government, with the introduction of the New Zealand Biodiversity Strategy (Anon 2000). Habitat loss, browsing and grazing, weed encroachment, and lack of legal protection are identified as the top four threats to New Zealand's nationally threatened vascular plant species (Dopson et al. 1999). All of these processes have occurred in New Zealand's South Island tussock grasslands, and continue to influence plant community dynamics. Large areas of tussock grasslands have been, and continue to be, modified by human activities for pastoral farming, which has led to a loss of habitat for many native grassland species. Low elevation areas have been especially affected (Walker et al. 2006). These areas are browsed and grazed by introduced mammals where populations of the most palatable native plants can be adversely affected (e.g., Mark 1965a, Gruner and Norton 2006). Grazing, combined with invasions by exotic species, are key threats to native species biodiversity in South Island tussock grasslands (Rose and Platt 1992, Mark 1993, Walker 2000). This is a concern because tussock grasslands are under-represented in the conservation estate (Mark and McLennan 2005), especially at low elevations (Walker et al. 2006). Understanding changes occurring in tussock grasslands within both conservation and pastoral tenure are therefore important (Norton 2001).

New Zealand's tussock grasslands are thought to be becoming more degraded and dominated by exotic species (Treskonova 1991, Rose et al. 1995, Walker et al. 2006). This degradation is considered to be largely due to agricultural practices and management (Mark 1965a, Walker

2000, Rose et al. 2004, Norton et al. 2006). Degradation is often measured as a decline in *Chionochloa* cover, and an increase in *Hieracium* spp. (Gibson and Bosch 1996). However, it is important to consider other aspects of the vegetation. A community-level approach to changes in plant species in tussock grasslands allows us to investigate changes at a higher level of biological organisation, while giving us the ability to focus on changes that have occurred in key species and species groups.

1.1. Management and tenure of tussock grasslands

O'Connor (1981) recognised two phases in tussock grassland management in the South Island. From European settlement to the 1950s there was the "Exploitative pastoralism phase" and then from the 1950s to the present there was the "Range Restoration phase". During the exploitative phase, the Crown retained ownership of all high country areas. This was divided and leased to be farmed on 11-year non-renewable leases (Mark and McLennan 2005). These short-term leases encouraged unsustainable management practices, where land was burned regularly and grazed heavily (Zotov 1938, O'Connor 1981). During this time, grasslands became highly degraded. For example, the total vegetation cover in the Upper Clutha in the early 1950s was less than 7%, leading to low pastoral and primary production (Connor 1964, O'Connor 1981).

The 1950s marked the beginning of the "Range Restoration phase", and occurred as a result of the 1948 Land Act being passed, which continues to apply today. The Land Act extended leases to 33-year periods and made them renewable (Mark and McLennan 2005). Sustainable practices were encouraged because lessees had the potential to maintain the land for an indefinite period of time, and there were also more stringent restrictions on stocking rates, burning and oversowing with exotic plants (Sewell 1952, O'Connor 1981). Even after this effort to encourage sustainable farming practices, research continued to show that tussock grasslands were becoming degraded over time, with low abundances and cover of *Chionochloa* species and increases in exotic weeds (Connor 1992b, Dickinson et al. 1992, Rose et al. 1995, Mark and McLennan 2005). This may have been due to the Government providing subsidies to farmers between the 1960s and the 1980s to fertilise and oversow land in pastoral tenure to prevent soil erosion (O'Connor 2003).

The Tenure Review process aimed to reverse this pattern of degradation. Under the 1998 Crown Pastoral Lease Act, Tenure Review takes some land out of pastoral lease and puts it in

to the public conservation estate. This process, among other things, aims to promote ecologically sustainable management of high country farms and retain areas with high conservation or cultural values in Crown ownership (Land Information New Zealand 2003). Each pastoral lease that undergoes tenure review is essentially divided and distributed to different parties. Areas that have high conservation value, which have high cultural, aesthetic or biodiversity values, go into Crown management to be managed for conservation, i.e. they are put into conservation tenure. In general, this means that they will no longer be grazed, unless the lessee applies for a grazing concession under special circumstances. Other areas that are productive and useful for pastoral farming go into freehold management. These areas generally continue to be farmed, but owners are not restricted to what they can do with the land except under restrictions from government legislation such as the 1991 Resource Management Act. The voluntary process of Tenure Review appears to be relatively popular among pastoral lessees. At July 2007, 61% (185 out of 303) of all Crown Pastoral Lease properties were at some stage of the Tenure Review process. Of these, 16% (or 48 out of 303) had been completed (Anon 2007).

Grazing is an important factor maintaining tussock grassland plant communities (Allen et al. 1995). Removing sheep grazing from areas that are highly modified and have been grazed for over a century can have dramatic impacts on the vegetation and its dynamics. For example, snow tussock populations have been shown to recover significantly after grazing has stopped (Dickinson et al. 1992, Rose and Platt 1992, Lee et al. 1993, Duncan et al. 2001, Meurk et al. 2002). Rose et al. (1995) showed that common native species in short-tussock grasslands were more abundant in retired areas after 25 years. However, other studies have documented increases in exotic species because these fast-growing species are no longer suppressed by herbivory (Norton 1988, Meurk et al. 1989, Lord 1990, Walker 2000). This is the opposite of the aims of Tenure Review and indicates that removing grazing alone may not increase native biodiversity or maintain tussock grassland areas (Norton 1988, Meurk et al. 1989, Calder et al. 1992, Roper-Lindsay 2000). Areas in conservation tenure are also unlikely to be burned, which may actually be necessary to maintain some native tussock grasslands (Calder et al. 1992). However, Tenure Review is a relatively new process, and the long-term implications of removing sheep grazing and burning from tussock grasslands are yet to be known.

Species composition and distribution in tussock grasslands have been shown to be strongly related to environmental variables, especially elevation (Wilson et al. 1989, Rose et al. 1998), and soil chemistry (Archer 1973, Allen et al. 1997, Rose et al. 1998). However, it is unclear

how these factors are related to temporal dynamics in tussock grasslands. This is mainly because most long term studies in tussock grasslands are relatively localised, and fail to encompass the wide range of environmental conditions over which tussock grasslands occur (e.g. Rose et al. 1995, Mark and Dickinson 2003, Rose et al. 2004). Furthermore, because those studies are not based on a standard method for monitoring tussock grasslands we cannot pool the data from each of these studies to gain an understanding of tussock grasslands as a whole, which greatly hinders our understanding of vegetation dynamics in tussock grasslands (Allen 1993). In addition, most monitoring studies have been of short duration (10 years or less) (Walker 2000, Grove et al. 2002, Meurk et al. 2002). The present study overcomes both of these issues by using standard sampling methods over 24 years, and encompassing a wide geographic area of tussock grasslands.

2. Re-measurement of 90 permanently-marked vegetation transects in tussock grasslands

This thesis used vascular plant community data collected from 90 permanently-marked transects throughout Canterbury and Otago in New Zealand's South Island tussock grasslands. This is a subset of transects from a larger data set of 142 transects, which were established between 1982 and 1986 (first measurement). Each transect was 100 m long, and a 0.25 m^2 quadrat was placed every two metres. The presence of each species that was overhanging or rooted within the quadrat was recorded. The transects were re-measured between 1993 and 1999, and a decline in species richness was reported between these measurements at both the small scale, within quadrats of 0.25 m^2, and at the large scale, within 100 m transects, sampling an area of 12.5 m^2 (Duncan et al. 2001). For this study, land was categorised into one of two tenure categories: conservation tenure, which is administered by the Department of Conservation, and pastoral tenure, which is land that is managed for grazing by domestic stock. Pastoral tenure includes land that is in pastoral lease from the government, and land that is in freehold and owned outright.

The central theme of this thesis was the investigation of temporal changes in tussock grassland vascular plant communities. Initially changes in species richness were examined using methods comparable to Duncan et al. (2001). Secondly, spatial variation in species composition was described, and thirdly, a refined data set was used to assess changes in species composition that had occurred in short- and tall-tussock grassland communities.

2.1. Aim and objectives

The aim of this study was to investigate changes in species richness and composition in tussock grasslands over time, and to relate these changes to environmental variables and land tenure. This was addressed by three objectives.

Changes in species richness

Objective: To describe and explain the temporal variation in tussock grassland vascular plant species richness in Canterbury and Otago between the first and second measurements, and between the second and third measurements. This was achieved by:

1. Determining whether vascular species richness continued to decline in these grasslands between the second and third measurements, as it did between the first and second measurements at both the small scale and the large scale (as shown by Duncan et al. 2001).
2. Determining whether changes in species richness differed between transects in conservation tenure and pastoral tenure.
3. Determining which of the measured environmental variables best predicted changes in species richness.

Species composition

Objective: To describe spatial variation in vascular plant species composition in tussock grasslands throughout Canterbury and Otago, and to relate this variation to measured environmental variables. This was achieved by:

1. Classifying vascular plant composition communities that were present on these transects at all measurements.
2. Investigating how spatial variation in vascular plant species composition was related to measured environmental variables.

Changes in species composition

Objective: To describe and explain temporal changes in species composition that have occurred in tussock grasslands throughout Canterbury and Otago, and to investigate how these changes related to land tenure. This was achieved by:

1. Assessing the importance of each environmental variable for describing species composition at each measurement, and investigating how the importance of each variable may have changed over time.
2. Describing the patterns of temporal changes in species composition in terms of the nature and amount of change.
3. Investigating how the nature and amount of compositional change related to land tenure, property, plant community type, rock type, soil type, burning occurrence between the first and second measurements, elevation and solar radiation.

Chapter 2: Changes in Vascular Plant Species Richness of South Island Tussock Grasslands

1. Abstract

New Zealand's South Island tussock grasslands are highly modified. This is largely due to the effects of fire, agricultural development, introduced pests and herbivores, and subsequent invasion by exotic weeds. Recently, many areas have been retired from grazing, which is likely to result in significant changes in the vegetation; however, what these changes will be is unclear. This chapter describes changes in species richness that have occurred on 90 permanently marked transects throughout Canterbury and Otago. Transects were measured on three occassions: between 1982 and 1986 (first measurement), between 1993 and 1998 (second measurement) and between 2005 and 2006 (third measurement). Species richness declined significantly at the small (0.25 m^2) scale between the first and second measurements from 8.22 to 6.62 species. Species richness then increased significantly to 7.74 at the third measurement. Changes in species richness were not driven by changes in exotic species richness and occurred independently of whether the transects were in conservation or pastoral tenure. Linear mixed-effects models revealed that elevation and rock type were significant predictors of changes in species richness at the small scale. These results suggest that over the past 24 years changes in species richness in South Island tussock grasslands have occurred independently of management.

2. Introduction

Widespread burning combined with introductions of exotic plants and animals for pastoralism in the South Island high country has led to large areas of induced tussock grasslands (Zotov 1938, O'Connor 1982, Mark 1993). The highly modified nature of these ecosystems has made vegetation change in tussock grasslands the subject of many ecological studies (e.g., Treskonova 1991, Mark and Dickinson 2003, Rose et al. 2004). Vegetation change can be investigated by looking at changes in the number of species present over time, i.e. changes in species richness. This analysis can be made more powerful by looking at the changes in numbers of species with similar ecological roles, because they are likely to respond similarly to changes in the environment and to disturbances (Lavorel et al. 1997).

Previous studies in tussock grasslands have reported declines in species richness, which is often attributed to effects of intensive pastoral management and grazing (Lord 1990, Connor 1992a, Dickinson et al. 1992, Grove et al. 2002). However, species richness can also decrease in areas that are in conservation tenure and are no longer grazed by domestic stock (e.g., Mark and Dickinson 2003), which can be because they become dominated by a few exotic species (Norton 1988, Meurk et al. 1989, Lord 1990, Walker 2000).

There have been some rare cases where species richness has increased in tussock grasslands. Walker (2000) recorded an increase in species richness in the Flat Top Hill Conservation Area in Central Otago between 1993 and 1997. This increase was attributed to increases in exotic species richness which were previously suppressed by grazing, combined with high rainfall throughout the sampling period. Other studies, using between 10 and 37 years of data throughout South Island tussock grasslands have shown increases in exotic species richness and concurrent declines in native species richness, indicating that this may be a widespread trend over a range of environmental conditions (Rose et al. 1995, Meurk et al. 2002, Rose et al. 2004).

Monitoring the changes in species richness and elucidating the drivers of those changes over a long time are important for understanding temporal vegetation dynamics and making informed management decisions. Between 1982 and 1986 142 permanently-marked vegetation transects were established in tussock grasslands across Canterbury and Otago. Each transect was 100 m long, and consisted of 50, 0.25 m^2 quadrats laid every two metres. All vascular species that were overhanging or rooted in the quadrat were recorded. The transects were re-measured between 1993 and 1999, and a decline in species richness was reported between these measurements at both a small scale, within quadrats of 0.25 m^2, and at a large scale, within 100 m transects, sampling an area of 12.5 m^2 (Duncan et al. 2001). Between 2005 and 2006, 90 of these transects were remeasured in order to ask: (1) Has vascular species richness continued to decline between the second and third measurements, as it did between the first and second measurements at both the small scale and large scale? (2) Were changes in species richness between measurements different for transects in conservation tenure compared with transects in pastoral tenure? (3) Are there differences in the way species richness has changed between measurements, and are those differences predictable from the measured environmental variables?

3. Methods

3.1. Study area

One-hundred and forty-two permanently-marked vegetation transects were set up on 19 properties in areas of tussock grassland across Canterbury and Otago in the South Island of New Zealand between 1982 and 1986 (first measurement) (Figure 1). Transects were clustered in space by property, with the number of transects on each property ranging from one to ten. The transects were set-up by the Department of Lands and Survey, and placed to be representative of the general vegetation in the area (C. Jensen, personal communication, 2005). The transects covered a wide range of tussock grassland environments. These transects were re-measured between 1993 and 1998 (second measurement).

Due to time constraints only 90 of the 142 transects were remeasured in 2005-2006 (third measurement) (Figure 2). These 90 transects were chosen based on the month of measurement and the time available to do the fieldwork. The 90 transects are a representative subset of the 142 transects in that they covered much of the environmental and geographical variation encompassed by the original 142 transects (Figures 1, 3 and 4). In addition, the change in small scale (0.25 m^2) species richness between the first and second measurements for the subset of 90 transects follows a similar distribution for all 142 transects (Figure 5), suggesting that the 90 transects are a representative sample with regard to change in species richness.

The 90 transects were placed on land in both conservation and pastoral tenure and some of the sampled properties changed tenure throughout the 24-year period of measurements (Table 1). Grouping the transects by tenure is only a coarse method of classifying by management, where we assume that transects in conservation tenure have been ungrazed by domestic stock. Furthermore, records of stock numbers were not obtained for the transects in pastoral tenure, meaning that no inferences can made about the effects of grazing intensity on species richness in tussock grasslands in this study.

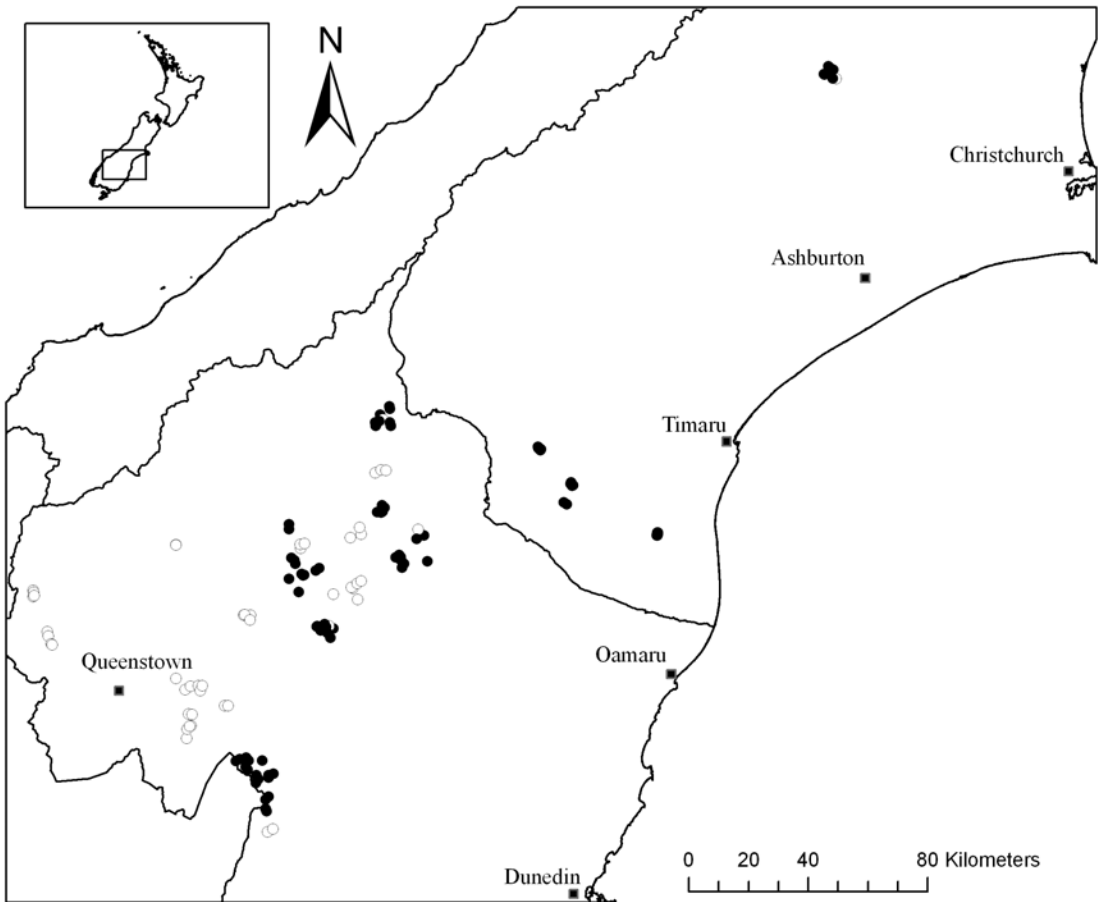

Figure 1: Location of 142 transects in tussock grasslands across Canterbury and Otago. Filled circles represent 90 transects that were remeasured in 2005-6; open circles represent transects that were not remeasured in 2005-6.

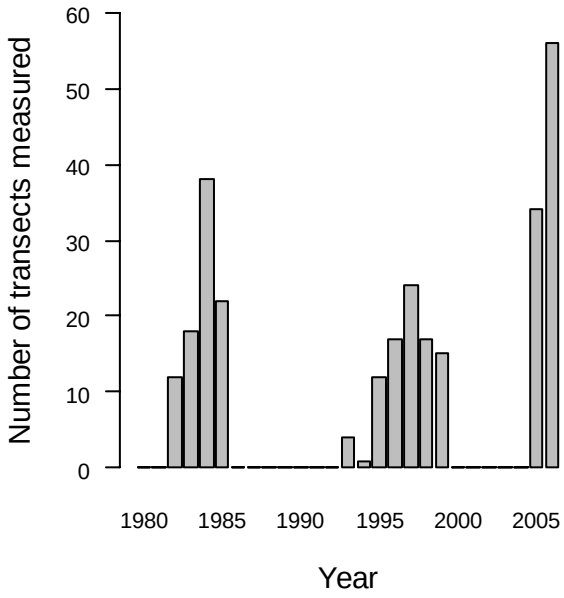

Figure 2: Distribution of the dates of transect measurement for each of the three measurements for the subset of 90 transects in tussock grasslands of Canterbury and Otago. Measurement 1: 1982-1985, measurement 2: 1993-1999, measurement 3: 2005-2006. Transects were established between November and March. Most transects were remeasured in the same month that they were initially established.

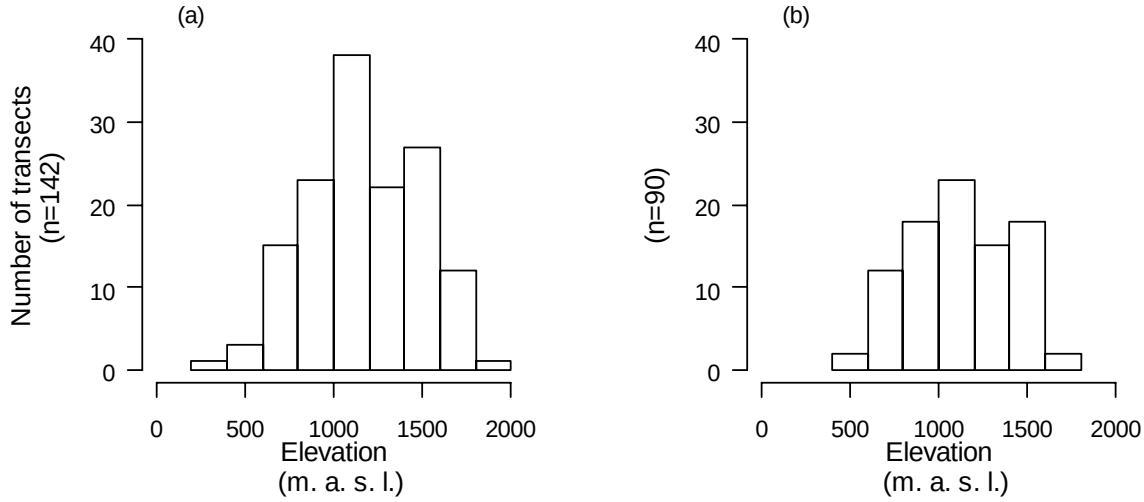

Figure 3: Frequency histograms showing the number of transects at different elevations (metres above sea level) for all 142 transects (a) and the subset of 90 transects measured in 2005-2006 (b).

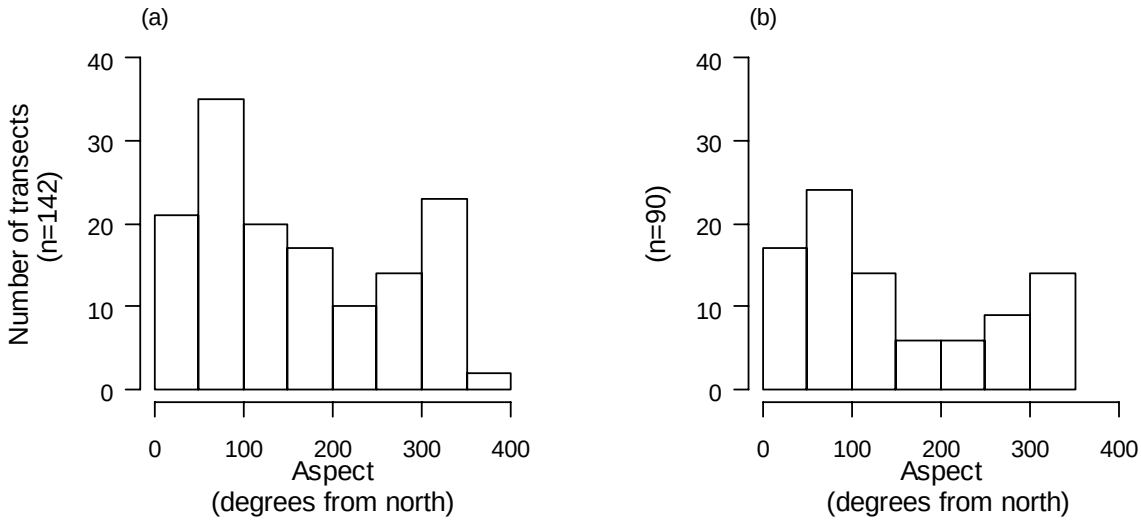

Figure 4: Frequency histograms showing the number of transects at different aspects (degrees from north) for all 142 transects (a) and the subset of 90 transects measured in 2005-2006 (b).

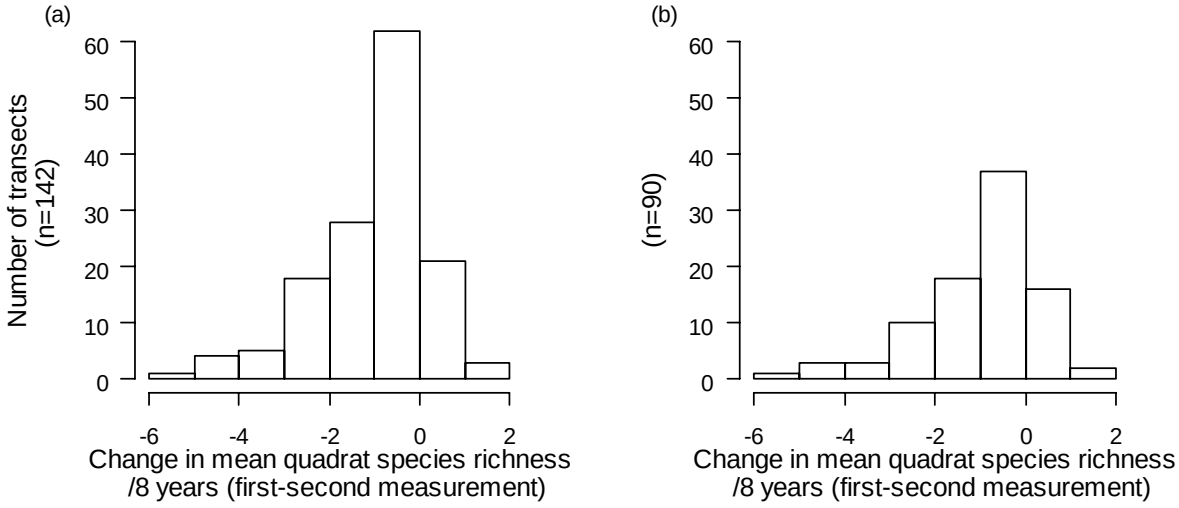

Figure 5: Frequency histograms showing the change in mean quadrat species richness for all vascular species between the first and second measurements per eight years for all 142 transects (a), and for the subset of 90 transects remeasured in 2005-2006 (b).

Table 1: Number of transects in each tenure category at each measurement for 90 transects. First measurement: 1982-1986, second measurement: 1993-1999, third measurement: 2005-2006.

Number of transects in tenure	First measurement	Second measurement	Third measurement
Conservation	21	26	36
Pastoral	69	64	54

3.2. Data collection

Accurate relocation of each transect was possible from detailed location information that was recorded at the first measurement. Co-ordinates (New Zealand map grid system) for each transect were recorded and marked on a map of each property. In the field, transects were marked at both ends with a white fibreglass pole. Cattle ear-tags were attached to the bottom pole, with the transect number written on it in permanent ink. Detailed field notes contained information about how to access each transect, and their locations in relation to key landmarks. Photographs were taken at each measurement. These showed the location of transects within the landscape, and looking up and down each transect, which were used to relocate and set-up transects. These photographs were used to accurately set up transects if one or both of the fibreglass poles were missing. Missing poles were replaced where possible. Most transects had metal pegs in the ground at 10, 30, 50, 70 and 90 m along the transect, which were used to take stereophotographs at the first measurement. Although stereophotos were not taken at the second or third measurements, these pegs enabled precise relocation of the transect line. Upon relocation at the third measurement, the position of the top and bottom poles were recorded using a global positioning systems device (GPS). At the third measurement, four transects were not able to be accurately relocated using the combination of information outlined, and so they were not re-measured.

Each transect was 100 m long and comprised 50 square 0.25 m^2 quadrats regularly placed at two metre intervals. At the first measurement, the presence of each vascular plant species inside each quadrat, including overhanging species, was recorded. At the second and third measurements, each vascular plant species present was given a cover score between one and six within the quadrat, which represented covers of <1%, 2-5%, 6-25%, 26-50%, 51-75%, and 76-100% respectively. The percent cover of bare ground, rock, litter and vegetation cover was estimated visually to the nearest 5% in each quadrat at each measurement. Hybridisation

between *Chionochloa* species at some sites meant that *Chionochloa* could not always be identified to species level (C. Jensen, personal communication 2007). For this reason, all *Chionochloa* species were pooled into one species for all measurements. These species included *Chionochloa flavescens, C. rigida* and *C. macra*.

Species identifications were consistent across time, because the same botanist was involved in identifications at each measurement. Carol Jensen set-up the transects, re-measured them the second time, and also trained the field team in species identification for the third measurement. At the third measurement, if the field team could not identify a plant, specimens were collected and pressed and later identified from herbarium specimens or taken to C. Jensen for identification. C. Jensen also re-measured ten transects in 2005 independently of the field team, which are included in the 90 transects. Seasonal effects in species identifications were mitigated by always re-measuring each transect in summer, and during the same month that it was originally set up, as much as possible. These consistent species identifications ensured that data collected at each measurement were comparable. Species that had their names changed over the period of measurements were changed to the most recent name before analysis.

Soil type (brown, including yellow-brown soils, or grey, including brown-grey and yellow-grey soils) and rock type (greywacke or schist) were obtained for each transect from mapped data from general soil surveys of the South Island (New Zealand Soil Bureau 1968). Using the GPS reference for the bottom pole of each transect, the elevation, aspect and slope were obtained from a 25×25 m resolution digital elevation model (DEM) provided by Landcare Research, using ArcGIS 9.1 (ESRI 2005). A solar radiation index, which is the potential amount of radiation from the sun that a transect may receive per year, was calculated from latitude, aspect and slope (Kaufmann and Weatherred 1982). Tenure of each transect (pastoral or conservation) was obtained from Land Information New Zealand and the Department of Conservation records. To assess whether a transect had been burned between the first and second measurements the current lessee was asked or the vegetation was assessed for signs of burning. This was not done at the third measurement due to time restrictions. A representative soil sample was taken along the transect at the third measurement: five soil samples, at depths of 10 cm, were taken at regular 20 m intervals along each transect and then pooled. Samples were dried and analysed for pH, calcium, phosphorus, potassium, sulphur, magnesium, and sodium by New Zealand Labs using standard techniques (Kay and Hill 1998). These soil parameters gave a good overview of the basic chemical composition of the soil in tussock

grasslands (Leo Condron, personal communication 2005). Unfortunately, soil nitrogen was not measured because the soils were stored for long periods while away doing field work. This would have made any analyses inaccurate (Leo Condron, personal communication 2005). Soil parameters were not measured in previous measurements, in the hope that these may provide a baseline for future remeasurements.

Each vascular plant species was classified by its life history characteristics in three ways (following Duncan et al. 2001):

1. Growth form, in terms of woody, grasses excluding *Chionochloa* spp., small herbs less than 2 cm tall, large herbs greater than 2 cm tall, ferns, rushes and sedges, *Hieracium* spp., or *Chionochloa* spp.. *Hieracium* spp. and *Chionochloa* spp. were considered separately because they may have disproportionate effects on species richness (Treskonova 1991, Scott 1993).
2. Longevity: whether plants were annual or perennial.
3. Origin: whether plants were native or introduced. Analyses using origin excluded *Hieracium* spp. because they have large impacts on changes in tussock grasslands, and the effect of *Hieracium* alone could overshadow the effects of other exotic species (Duncan et al. 2001). *Hieracium lepidulum, H. pilosella*, and *H. praeltum* were the most common *Hieracium* species on these transects, but *H. auranticum* and *H. caespitosa* were also present.

3.3. Data analysis

3.3.1. Changes in mean quadrat species richness

For each transect at each measurement, mean quadrat species richness was calculated by summing the total number of quadrats that each species occurred in, summing this for all species on a transect, and then dividing by 50 (the number of quadrats on a transect). Change in mean quadrat species richness between the first and second measurements was calculated for each transect by subtracting mean quadrat species richness at the first measurement from mean quadrat species richness at the second measurement. Similarly, change in mean quadrat species richness between the second and third measurements, was calculated as mean quadrat species richness at the second measurement subtracted from mean quadrat species richness at the third measurement. These changes in mean quadrat species richness for each transect were standardised to a rate of change per eight years by dividing the change in species richness by the interval between measurements (in years) and then multiplying by eight. This was because the mean interval between the first and second measurements was 13 years, while the mean interval between the second and third measurements was 8.72 years.

A significant change in mean quadrat species richness ($P < 0.05$) for all species was tested for by performing a two-tailed, one-sample *t*-test on the change in mean quadrat species richness per eight years between the first and second measurements, and then between the second and third measurements. Significant changes in mean quadrat species richness for each group of plant species, classified in terms of origin, longevity and growth form, were also investigated using two-tailed, one-sample *t*-tests ($P < 0.05$) on the change in mean quadrat species richness per eight years between the first and second measurements, and between the second and third measurements.

Transects were categorised by their tenure (conservation or pastoral) at the second measurement so that there were the same number of transects in each tenure category for all analyses. There was low variation in the number of years since grazing had ceased, so it made no difference using a categorical variable. Significant changes in mean quadrat species richness for each tenure category were calculated using two-tailed one-sample *t*-tests ($P < 0.05$) on the change in mean quadrat species richness per eight years between the first and second measurements, and between the second and third measurements. A two-tailed two-sample *t*-test was used to assess whether transects in different tenure categories showed similar changes in mean quadrat species richness between measurements. Tenure at the second measurement was used so that the number of transects in each category was the same for each test. To investigate whether changes in native and exotic species richness differed according to tenure, two-tailed one-sample *t*-tests were performed on changes in mean quadrat species richness in native and exotic species along transects under conservation and pastoral tenure.

3.3.2. Predictors of mean quadrat species richness change for each time period: linear mixed-effects models

To find the best environmental predictors of change in mean quadrat species richness, two models were built to predict change at each of the two time intervals: between the first and second measurements (first time interval), and between the second and third measurements (second time interval). The response variable was change in mean quadrat species richness, excluding *Chionochloa* and *Hieracium* species, as these were included in the model as potential predictor variables.

Transects clustered together in space are likely to be more similar to each other than those further apart because they experience the same environmental conditions, i.e. they are spatially autocorrelated (Legendre 1993). To account for this, "property" was included as a random effect in the model. This means that the variation in transects within a property is taken into account in assessing the amount of variation that is explained by other variables in the model. The remaining explanatory variables that are explicitly tested for are called fixed effects (Crawley 2002), and are the environmental variables recorded at each transect.

For all 90 transects, 15 environmental variables were initially considered as potential predictors of change in mean quadrat species richness between measurements (Table 2). Soil chemistry variables were transformed to a logarithmic scale, which represents the differences in levels of elements in the soil in a more biologically meaningful way. For example, the difference between 1 and 10 mg per kg calcium is likely to have a greater effect on plant growth than the difference between 101 and 110 mg per kg calcium in the soil, because it is already present in higher amounts. These differences are more accurately represented on a log scale which better represents the relationship between changes in the amount of calcium when it is at lower absolute concentrations (Palmer 1993). Relationships between continuous and categorical variables were assessed using box plots, and relationships between categorical variables were assessed using tables. Strongly correlated continuous variables were excluded, based on Pearson's correlation coefficients, reducing the number of potential predictors to eight.

Each of the eight potential predictors was put into a linear mixed-effects model on its own as a fixed effect, with property as a random effect. If it was a significant predictor ($P < 0.05$) on its own for either time interval it was put into the maximal model, i.e. the model that contains all of the potential predictor variables (Crawley 2002) (Table 2). The minimum adequate model for species richness change was attained by stepwise backward selection, where the least significant predictor was omitted and the model was re-run iteratively until all remaining variables explained a significant amount of variation in change in species richness (Crawley 2002). A predictor was retained in the model if it explained a significant amount of variation in mean quadrat species richness change when added to the model last ($P < 0.05$).

3.3.3. Changes in total transect species richness

The total number of species found across all quadrats on each transect was summed, providing a measure of total transect species richness. The change in total transect species richness between the first and second measurements was calculated by subtracting total transect species richness at the second measurement from the total at the first measurement. Similarly, change in total transect species richness between the second and third measurements was calculated by subtracting total transect species richness at the second measurement from total transect species richness at the third measurement. Change in total transect species richness was divided by the interval in years between measurements and then multiplied by eight, providing a standard measure of change in total transect species richness per eight years for each transect.

Significant changes in total transect species richness ($P < 0.05$) were tested for by using a two-tailed one-sample *t*-test on the change in total transect species richness per eight years for both time intervals. Changes in total transect species richness of species groups classified in terms of origin, longevity, and growth form were also assessed using two-tailed one-sample *t*-tests ($P < 0.05$).

Corrections for multiple *t*-tests performed on the same data were done using the Bonferonni correction (Crawley 2002). All statistical analyses were performed using R version 2.5.0 (R Core Development Team 2007), and mixed-effects models were run using the Linear and Nonlinear Mixed Effects Models (nlme) package (Pinheiro et al. 2006).

Table 2: Environmental variables that were considered as potential predictor variables in the linear mixed effects models for change in mean quadrat species richness between measurements. Variables marked with * indicate those that were significant predictors in a mixed model alone, and were included in the maximal model (see text for details).

Variable	Units / Levels
Change in vegetation cover between measurements	Increased Decreased
Burning history between first and second measurements	burnt not burnt
Elevation *	metres above sea level
Change in mean quadrat *Chionochloa* species richness between measurements *	increased decreased not present
Change in mean quadrat *Hieracium* species richness between measurements *	increased decreased not present
Tenure at first, second or third measurement	conservation pastoral
Rock type *	greywacke schist
Soil type *	brown (yellow-brown soils) grey (brown-grey and yellow-grey soils)
Solar radiation *	Watts per square metre (W/m^2)
Log soil pH	pH units
Log soil calcium	log (me / 100 g)
Log soil magnesium	log (me / 100 g)
Log soil phosphorus	log (µg / ml)
Log soil potassium	log (me / 100 g)
Log soil sodium	log (me / 100 g)
Log soil sulphur	parts per million (Ppm)

4. Results

4.1. Changes in mean quadrat species richness

On these 90 transects over the three measurement times there were a total of 347 species recorded. Mean quadrat richness declined significantly during the first time interval and then increased significantly during the second time interval (Table 3). Most transects showed these patterns (Figure 6). Mean quadrat species richness at the third measurement was not significantly different from that at the first measurement, which shows that mean quadrat species richness had nearly recovered to pre-decline levels at the third measurement (two-sample *t*-test: $t = 1.14$, d.f. = 178, $P = 0.257$, equal variances, Figure 7).

Mean quadrat native species richness declined during the first time interval, and then increased during the second interval (Table 3, Figure 8). This contrasted with mean quadrat exotic species richness that declined during the first interval, but showed no significant change during the second interval (Table 3). Mean quadrat native species richness declined more than mean quadrat exotic species richness during the first time interval (two-sample t-test: $t = -4.79$, d.f. = 165, $P < 0.001$, unequal variances). However, mean quadrat native species richness then increased more than exotic species richness during the second time interval (two-sample *t*-test: $t = 4.16$, d.f. = 158, $P < 0.001$, unequal variances).

Mean quadrat perennial species richness declined significantly during the first interval, and then increased significantly during the second time interval. In contrast, mean quadrat annual species richness declined during both intervals, but this was only significant during the first time interval (Table 3, Figure 8).

Small herbs, large herbs and rushes/sedges all declined significantly in mean quadrat species richness during the first time interval, and then increased significantly during the second time interval. Conversely, mean quadrat *Hieracium* species richness increased between both the first and second time intervals (Table 3). Change in mean quadrat *Chionochloa* species richness over all measurements was not significant (Table 3, Figure 8). Mean quadrat grass species richness declined significantly during the first time interval, but did not change significantly during the second time interval. In contrast, changes in mean quadrat species richness for both woody and fern species were not significant during the first time interval, but then increased significantly during the second time interval (Table 3).

Table 3: Results of *t*-tests on the change in mean quadrat species richness per 8 years for 0.25 m^2 quadrats on 90 transects in tussock grasslands in Canterbury and Otago between each measurement. * *P* < 0.05, ** *P* < 0.01, * *P* < 0.001, ns = not significant, after Bonferroni correction for multiple comparisons.**

	First time interval		Second time interval	
Species group	**Change in mean quadrat species richness / 8 yrs Mean ± standard error**	***t*-value (n = 90)**	**Change in mean quadrat species richness / 8 yrs Mean ± standard error**	***t*-value (n = 90)**
All species	-0.98 ± 0.14	-7.20 ***	1.05 ± 0.17	6.15 ***
Origin				
Native species	-0.79 ± 0.10	-7.88 ***	0.84 ± 0.12	6.79 ***
Exotic species (excl. *Hieracium*)	-0.38 ± 0.07	-5.42 ***	0.05 ± 0.08	0.58 ns
Longevity				
Annual species	-0.27 ± 0.06	-4.23 ***	-0.07 ± 0.07	-1.04 ns
Perennial species	-0.74 ± 0.11	-6.96 ***	1.11 ± 0.13	8.32 ***
Growth form				
Hieracium species	0.20 ± 0.03	6.32 ***	0.18 ± 0.02	7.88 ***
Chionochloa species	0.02 ± 0.01	2.43 ns	0.01 ± 0.01	1.09 ns
Woody species	-0.003 ± 0.02	-0.20 ns	0.19 ± 0.02	8.07 ***
Grass species (excl. *Chionochloa*)	-0.26 ± 0.05	-5.78 ***	0.10 ± 0.05	1.85 ns
Large herb species (>2 cm tall)	-0.21 ± 0.04	-4.84 ***	0.18 ± 0.05	3.49 **
Small herb species (<2 cm tall)	-0.58 ± 0.06	-9.28 ***	0.28 ± 0.06	4.27 ***
Fern species	-0.02 ± 0.01	-2.96 ns	0.03 ± 0.01	3.24 ***
Rush / sedge species	-0.12 ± 0.02	-7.29 ***	0.14 ± 0.03	4.66 ***

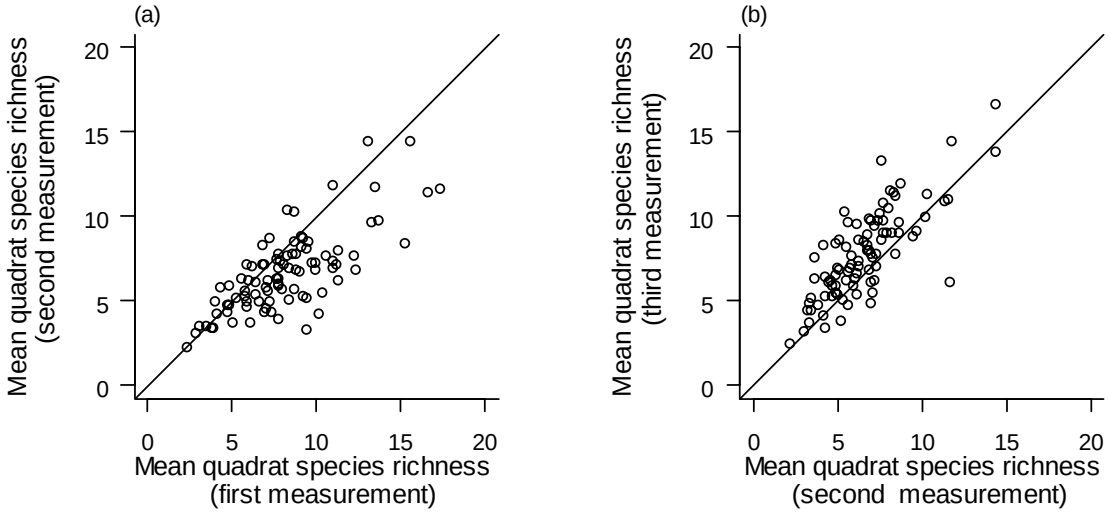

Figure 6: Mean quadrat species richness for 90 transects in tussock grasslands in Canterbury and Otago at the first and second measurements (a) and the second and third measurements (b). Points below the line are transects that have decreased in mean quadrat species richness between measurements, while those above the line have increased.

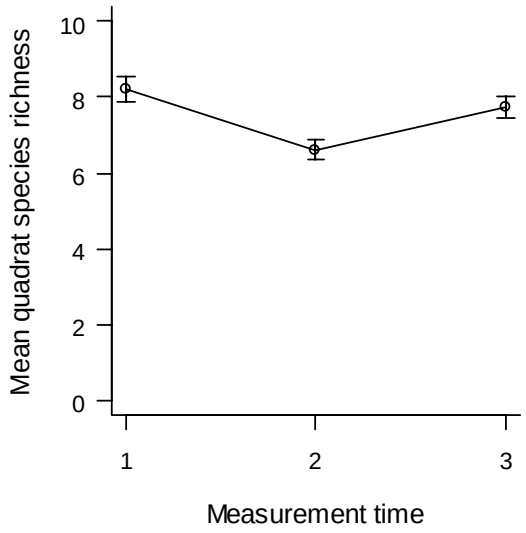

Figure 7: Mean quadrat species richness (± standard error) on 90 transects in tussock grasslands in Otago and Canterbury across the three measurement times. First measurement: 1982-1986, second measurement: 1993-1999, third measurement: 2005-2006. For the results of *t*-tests assessing the significance of changes in species richness between measurement times see Table 3.

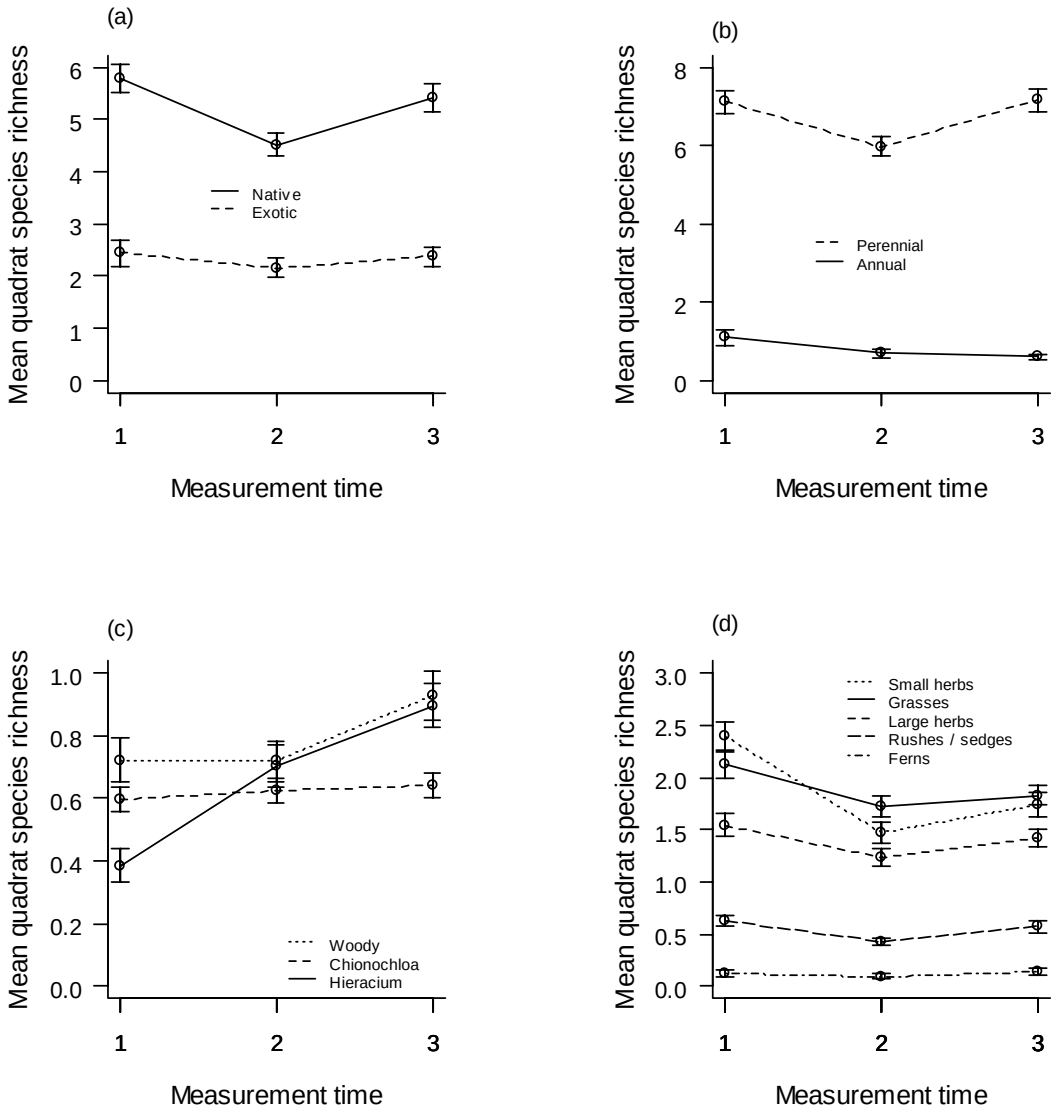

Figure 8: Mean quadrat species richness (± standard error) for each species group at each measurement in 0.25 m^2 quadrats for 90 transects in tussock grasslands in Canterbury and Otago. First measurement: 1982-1986, second measurement: 1993-1999, third measurement: 2005-2006. Native and exotic species (a), annual and perennial species (b), *Chionochloa* species, woody species, and *Hieracium* species (c), small herbs, grass species excluding *Chionochloa*, large herbs, rushes / sedges and ferns (d). For the results of *t*-tests assessing the significance of changes in species richness between measurement times see Table 3.

4.2. Changes in mean quadrat species richness in relation to tenure

Transects in pastoral tenure had significantly greater mean quadrat species richness than transects in conservation tenure at the first measurement (two-sample *t*-tests: first measurement: $t = 2.26$, d.f. = 34.59, $P = 0.0302$, unequal variances, second measurement: $t = 1.99$, d.f. = 88, $P = 0.0493$, equal variances, third measurement: $t = 1.12$, d.f. = 88, $P = 0.265$, equal variances, Figure 9).

Changes in mean quadrat species richness were similar on transects in both conservation and pastoral tenure, it decreased during the first time interval, and then increased to pre-decline levels at the third measurement regardless of tenure (two-sample *t*-tests: conservation land: $t = -0.35$, d.f. = 50, $P = 0.725$, equal variances; pastoral land: $t = 1.79$, d.f. = 126, $P = 0.076$, equal variances, Table 4, Figure 9).

In pastoral tenure, mean quadrat native species richness declined significantly during the first time interval, and then increased significantly during the second time interval. In conservation tenure mean quadrat native species richness increased significantly during the second time interval. The only significant change in mean quadrat exotic species richness by tenure was when it increased on conservation tenure during the second time interval (Table 5).

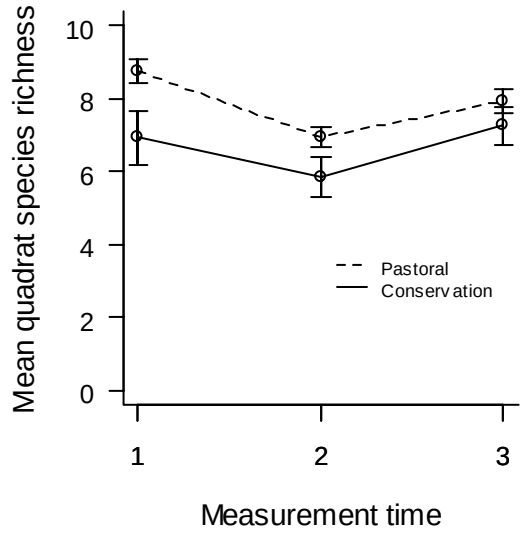

Figure 9: Mean quadrat species richness (± standard error) for each measurement on land in conservation tenure and in pastoral tenure at the second measurement for 0.25 m^2 quadrats in 90 tussock grassland transects in Canterbury and Otago. For significant differences in changes in mean quadrat species richness see Table 4.

Table 4: Results of *t*-tests on the change in species richness per 8 years for 0.25 m^2 quadrats on 90 tussock grassland transects in conservation or pastoral tenure in Canterbury and Otago between each measurement. Tests were done using tenure at the second measurement. n = number of transects at the second measurement. * *P* < 0.05, ** *P* < 0.01, * *P* < 0.001, ns = not significant, after Bonferroni adjustment for multiple comparisons.**

	First time interval		Second time interval	
Tenure	**Change in mean quadrat species richness / 8 yrs Mean ± standard error**	***t*-value**	**Change in mean quadrat species richness / 8 yrs Mean ± standard error**	***t*-value**
Conservation (n = 26)	-0.67 ± 0.25	-2.62 *	1.18 ± 0.25	4.71 ***
Pastoral (n = 64)	-1.10 ± 0.16	-6.95 ***	0.99 ± 0.22	4.57 ***

Table 5: Results of *t*-tests on the change in mean quadrat species richness per 8 years on transects in conservation or pastoral tenure for 0.25 m^2 quadrats in Canterbury and Otago between each measurement. * *P* < 0.05, ** *P* < 0.01, * *P* < 0.001, ns = not significant, after Bonferroni adjustment for multiple comparisons.**

	First time interval		Second time interval	
Tenure	**Change in mean quadrat species richness / 8 yrs Mean ± standard error**	***t*-value**	**Change in mean quadrat species richness / 8 yrs Mean ± standard error**	***t*-value**
Conservation				
Native species	-0.58 ± 0.21	-2.73 ns	1.01 ± 0.22	4.60 ***
Exotic species (incl. *Hieracium*)	-0.09 ± 0.06	-1.62 ns	0.18 ± 0.05	3.42 *
Pastoral				
Native species	-0.88 ± 0.11	-7.88 ***	0.77 ± 0.15	5.15 ***
Exotic species (incl. *Hieracium*)	-0.22 ± 0.11	-2.13 ns	0.23 ± 0.12	1.92 ns

4.3. Significant predictors of species richness change

One of the 90 transects had extreme values for log soil magnesium and log soil sodium. This transect was an alpine bog site and was removed from the analysis. The assumption of normality of the response variables demanded by mixed-effects models (Crawley 2002) were met without needing to transform the data for the change in mean quadrat species richness for both time intervals. There were 15 potential explanatory variables. Soil chemistry variables that correlated with elevation were omitted (log pH, log sulphur, log calcium, log magnesium, log potassium), and elevation was retained (Table 6). Of the eight remaining variables that were not highly correlated, six were significant predictors when put into the model on their own. These were put in to the maximal model for each time interval, which had all potential predictors included: change in mean quadrat *Chionochloa* species richness between measurements, change in mean quadrat *Hieracium* species richness between measurements, elevation, rock type, soil type, and solar radiation (Table 2).

After backward selection there were two significant predictors for the first time interval, and three for the second time interval (Table 7). Although direction of change in mean quadrat species richness differed for each period, both elevation and rock type were significant predictors of change in mean quadrat species richness for both models (Table 7, Figures 10 and 11). Generally, transects at higher elevations and on greywacke rock declined less in mean quadrat species richness during the first time interval, and increased more during the second time interval. However, these trends were weak (Figures 10 and 11). During the second time interval, transects where *Hieracium* increased also increased more in overall mean quadrat species richness (Figure 11).

Table 6: Pearson Product Moment Correlation coefficients for soil chemistry variables and elevation (n=89). * *P* < 0.05, ** *P* < 0.01, * *P* < 0.001, ns = not significant.**

Soil variables	Correlation coefficient with elevation (m.a.s.l.)
log phosphorus	0.08 ns
log pH	-0.69 ***
log sulphur	0.37 **
log calcium	-0.46 ***
log magnesium	-0.41 ***
log potassium	-0.49 ***
log sodium	0.19 ns

Table 7: Results from linear mixed-effects models of mean quadrat species richness change per 8 years for the two time intervals for 89 transects (excluding site with outlying soil variable). The *F*-value is based on when the variable is added to the model last. * *P* < 0.05, ** *P* < 0.01, * *P* < 0.001, ns = not significant.**

Variable	**df**	**Effect category**	**n**	**Model estimate ± standard error**	***F***
First time interval					
Intercept				-2.73 ± 0.52	27.70 ***
Elevation	1			-0.002 ± 0.0004	15.34 ***
Rock type	1	greywacke	53	0	7.94 *
		schist	36	-0.83 ± 0.29	
Second time interval					
Intercept				-0.98 ± 0.55	3.15 ns
Elevation	1			0.001 ± 0.0004	7.87 *
Rock type	1	greywacke	53	0	5.85 *
		schist	36	-0.67 ± 0.28	
Change in *Hieracium*	2	decreased		0	5.72 *
		increased		0.90 ± 0.34	
		none		-0.37 ± 0.54	

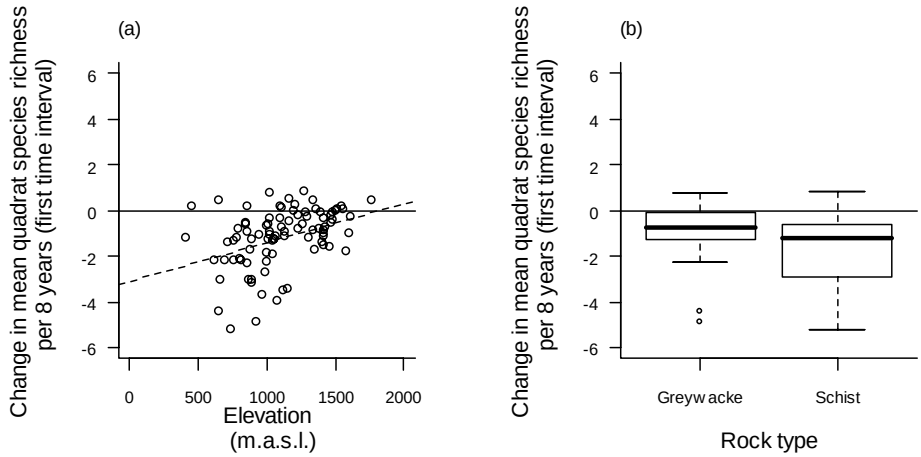

Figure 10: Significant predictors of change in mean quadrat species richness during the first time interval on 89 transects in tussock grasslands in Canterbury and Otago are elevation (metres above sea level, line of best fit is from linear mixed-effects model including only elevation) (a), and rock type (b).

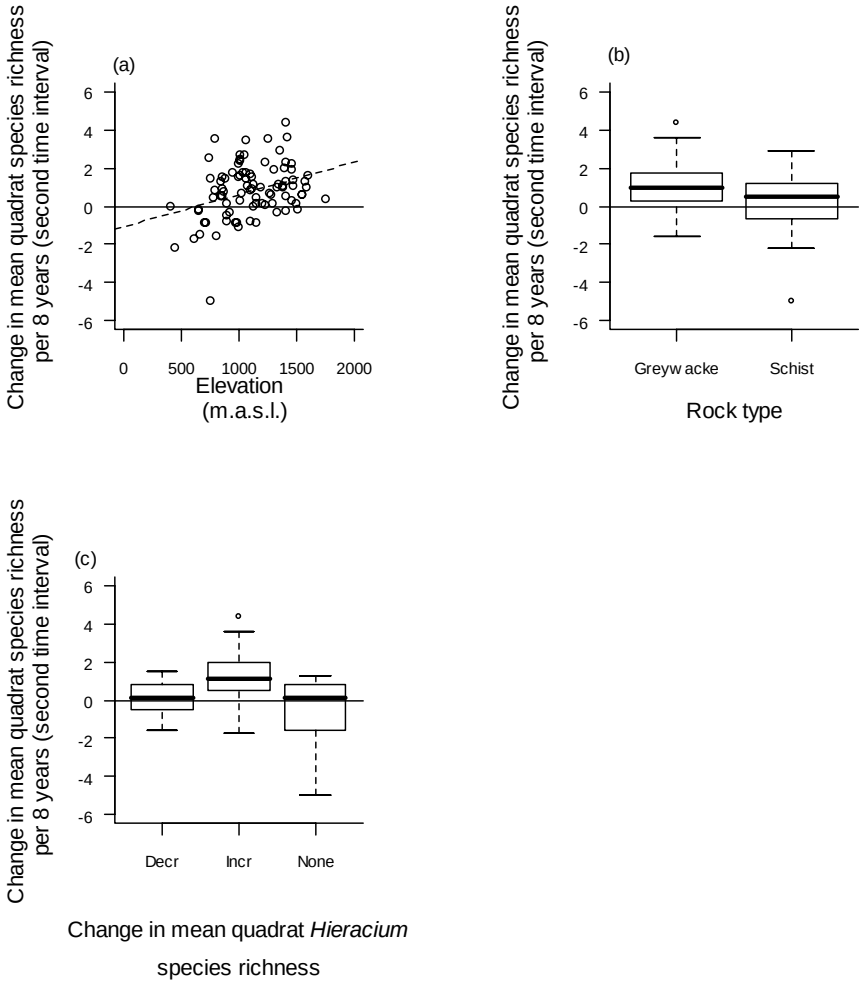

Figure 11: Significant predictors of change in mean quadrat species richness during the second time interval on 89 transects in tussock grasslands in Canterbury and Otago are elevation (metres above sea level, line of best fit is from linear mixed-effects model including only elevation) (a), rock type (b) and change in mean quadrat *Hieracium* species richness (c). Decr = decreased, Incr = increased, None = not present.

4.4. Changes in total transect species richness

Change in mean quadrat species richness was significantly correlated with change in total transect species richness for both time intervals (first time interval: r = 0.63, n = 90, $P < 0.001$, second time interval r = 0.54, n = 90, $P < 0.001$, Figure 12). Total transect species richness declined significantly during the first time interval, and then increased at the third measurement, although this was not significant (Table 8).

Both native and exotic species declined significantly in total transect species richness during the first time interval, but did not change significantly during the second time interval. Total transect perennial species richness declined significantly during the first time interval, and then increased significantly during the second time interval. Total transect annual species richness did not change significantly between either interval (Table 8).

Total transect *Hieracium* species richness increased significantly during both time intervals (Table 8). Total transect woody species richness did not change significantly during the first time interval, but increased significantly during the second time interval. Grass species and small herbs both declined significantly in total transect species richness during the first time interval, but did not change significantly during the second time interval. Changes in total transect species richness for *Chionochloa* spp., large herbs, ferns and rushes were not significant for either time interval.

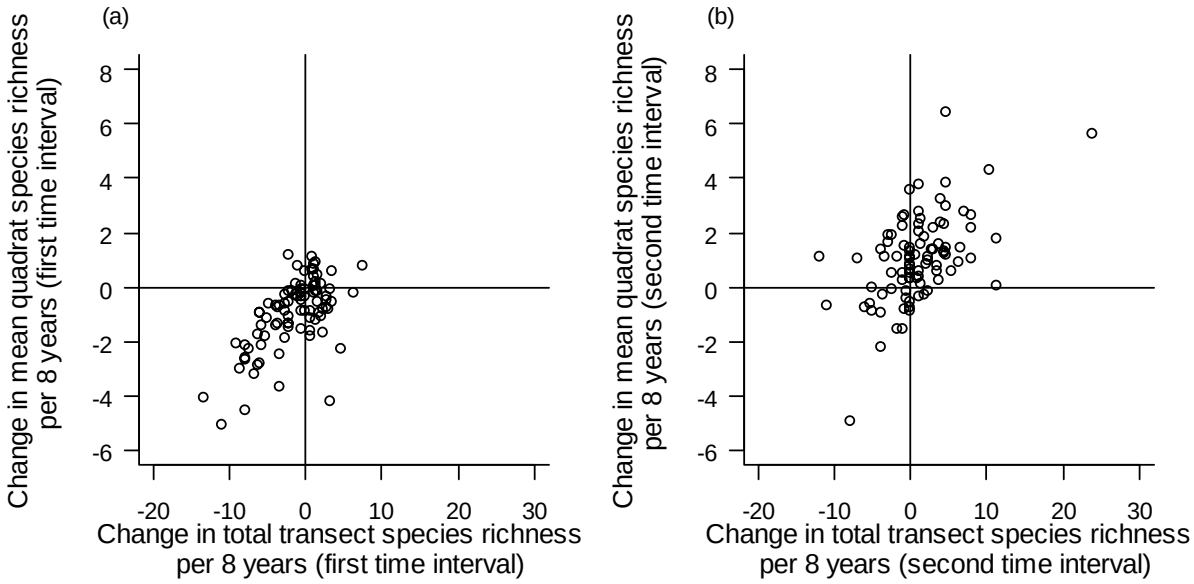

Figure 12: Relationship between change in mean quadrat species richness per 8 years and change in total transect species richness per 10 years for 90 transects in tussock grasslands in Canterbury and Otago.

Table 8: Results of *t*-tests on the change in total transect species richness per 8 years on 90 tussock grassland transects in Canterbury and Otago between each measurement. * * *P* < 0.05, ** *P* < 0.01, * *P* < 0.001, ns = not significant, after Bonferroni correction for multiple comparisons.**

	First – second measurement		Second – third measurement	
Species group	**Change in total transect species richness / 8 yrs Mean ± SE**	***t*-value (n = 90)**	**Change in total transect species richness / 8 yrs Mean ± SE**	***t*-value (n = 90)**
All species	-1.50 ± 0.41	-3.64 *	1.06 ± 0.51	2.05 ns
Origin				
Native species	-1.10 ± 0.29	-3.78 **	0.89 ± 0.39	2.26 ns
Exotic species (excl. *Hieracium*)	-0.73 ± 0.20	-3.59 *	-0.12 ± 0.19	-0.61 ns
Longevity				
Annual species	-0.47 ± 0.17	-2.73 ns	-0.28 ± 0.18	-1.57 ns
Perennial species	-1.05 ± 0.32	-3.33 *	1.32 ± 0.44	3.00 ns
Growth form				
Hieracium species	0.34 ± 0.06	6.09 ***	0.30 ± 0.09	3.45 *
Chionochloa species	-0.01 ± 0.02	-0.75 ns	0.01 ± 0.03	0.23 ns
Woody species	0.12 ± 0.08	1.41 ns	0.50 ± 0.12	4.05 **
Grass species (excl. *Chionochloa*)	-0.63 ± 0.17	-3.78 **	-0.20 ± 0.20	-1.02 ns
Large herb species (>2 cm tall)	-0.19 ± 0.18	-1.06 ns	0.14 ± 0.16	0.90 ns
Small herb species (<2 cm tall)	-1.21 ± 0.17	-7.16 ***	0.21 ± 0.25	0.83 ns
Fern species	0.02 ± 0.07	0.35 ns	0.09 ± 0.11	0.83 ns
Rush / sedge species	0.12 ± 0.06	2.10 ns	0.10 ± 0.09	1.16 ns

5. Discussion

5.1. Is species richness declining in these grasslands?

On these 90 transects in South Island tussock grasslands, species richness declined at both the small scale (0.25 m^2) and at the larger scale (100 m) during the first time interval, although this was only significant at the small scale (Tables 3 and 8, Figure 7). A closer look at this reveals that more species groups declined in species richness at the small scale than at the large scale (Tables 3 and 8). This is because population turnover is faster at small scales compared to large scales, and therefore species richness fluctuates more over time at small scales (Adler and Lauenroth 2003).

In the present study, species richness increased during the second time interval at both the small and large scales (Tables 3 and 8, Figure 7). I am aware of only one other study, which was on Flat Top Hill, that has reported a recent increase in species richness over four years in tussock grasslands (Walker 2000). Four years is a very short period of time in these communities, and it is difficult to know how strong this trend will be over the long term (Scott et al. 1988, Mark and Dickinson 2003). On the other hand, studies with measurements very far apart over time may fail to record fluctuations that occur in the short-term. For example, Treskonova's (1991) widely cited study looking at changes in *Hieracium* in the Mackenzie country was based on measurements that were 24-26 years apart. The present study and Walker's (2000) study show that changes in species richness do occur over shorter time intervals. Having long-term records with measurements at short intervals gives us a deeper understanding of the dynamics that are occurring in tussock grasslands. For example, over the longer term species richness could be declining, fluctuating or increasing, which would not be captured by two measurements that are 30 years apart if there are significant fluctuations in species richness over shorter time scales (Figure 13). Although measurements in the present study were between seven and fifteen years apart, they are short enough to be able to see relatively short-term changes that may be occurring in tussock grasslands (Hunter and Scott 1997).

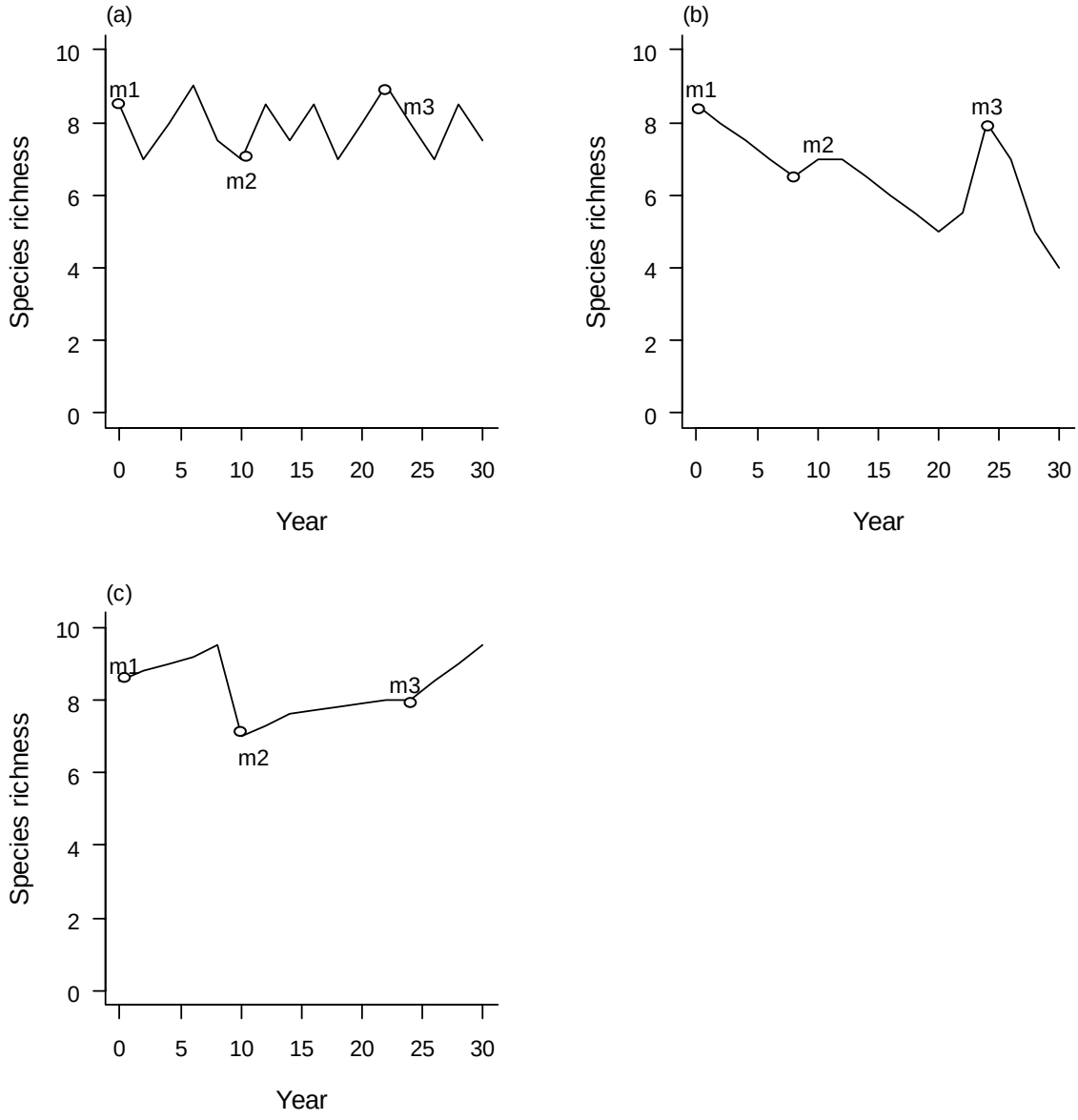

Figure 13: Three scenarios of how species richness may be changing in South Island tussock grasslands over the long-term, with short-term fluctuations. Species richness could be fluctuating (a), declining (b) or increasing (c). m1 = first measurement, m2 = second measurement, m3 = third measurement.

The pattern of decline and then increase in species richness observed in the present study is occurring over a wide geographic area (Figure 1) and across a range of environmental conditions (Figures 3 and 4). Although transects in the present study were not randomly located, the large geographic area and the range of topographies and elevations represented shows that the observed changes in species richness were widespread. Declines in species richness observed by others are generally in small geographic areas and reserves (Lord 1990, Dickinson et al. 1992, Grove et al. 2002, Mark and Dickinson 2003), and so may not be representative of tussock grasslands in general. In saying this, some species groups did not recover in mean quadrat species richness during the second time interval, in particular exotic species, annual species, and grasses.

Small herbs declined the most in mean quadrat species richness, and in total transect species richness during the first time interval, and then increased the most during the second time interval (Table 3, Figure 8). Small herbs are probably key drivers of species richness change because they account for 33% of all species on the transects. Being relatively small and fast-growing *r*-selected species (Begon et al. 1996), we would expect small herb populations to have a high turnover rate, explaining why their numbers are so varied across the three measurements. Small herbs were also drivers of change in species richness in tussock grasslands in the Black Rock Reserve (Dickinson et al. 1992). In the present study, the change in small herbs species richness does not seem to be driven by changes in other species groups, most of which showed similar changes over time (Figure 8). It is unlikely that small herb species were outcompeted by increasing *Hieracium* abundance during the first time interval, because they had increased by the third measurement even while *Hieracium* also increased in mean quadrat species richness.

There were five species of *Hieracium* on these transects: *Hieracium lepidulum, H. pilosella, H. praeltum*, and *H. auranticum* and *H. caespitosa*, which were less common. The increase in *Hieracium* species richness at both scales (Tables 3 and 8) is consistent with other studies (e.g., Treskonova 1991, Rose et al. 1998). During the first time interval, transects where mean quadrat *Hieracium* species richness increased did not decline more in overall mean quadrat species richness, where *Hieracium* spp. were excluded (two-sample *t*-test: $t = 0.40$, d.f. = 88, $P = 0.689$, equal variances). This was surprising because *Hieracium* has often been reported to become dominant in tussock grasslands and exclude the establishment of other species (Treskonova 1991, Duncan et al. 1997, Johnstone et al. 1999, Meurk et al. 2002, Rose et al.

2004). In addition, mean quadrat species richness, where *Hieracium* spp. were excluded, actually increased more on transects where *Hieracium* had increased significantly during the second time interval (two-sample *t*-test: $t = 2.78$, d.f. = 35, $P = 0.009$, unequal variances, Figure 11). These results are consistent with the idea that *Hieracium* invades and increases in areas regardless of original species composition or management (Rose et al. 2004).

Overall, *Chionochloa* species richness was relatively stable at both the transect and quadrat scales (Tables 3 and 8). All *Chionochloa* species were pooled, which means that this represents change in the abundance in an amalgam of several species, rather than all *Chionochloa* species. *Chionochloa* are long-lived and reproduce by mast seeding, i.e. rare, large synchronised seed events (Kelly et al. 1992), so there may have been few opportunities for *Chionochloa* to increase on these transects over the time if environmental conditions were not favourable for reproduction (Mark 1965c, Mark and Dickinson 2003). Furthermore, *Chionochloa* seedlings are highly palatable to sheep and hares, making regeneration by seed difficult where these mammals are present (Mark 1965a, Rose and Platt 1992, Lee et al. 1993).

Elevation and rock type were the best predictors of change in mean quadrat species richness; (Table 7). Transects that were at higher elevations decreased less in mean quadrat species richness during the first time interval, and then increased more during the second time interval (Figures 10 and 11). Low temperatures at high elevations lead to shorter growing seasons (Mark 1965b). This slows turnover in species populations, which makes changes in species richness slower and less-pronounced than at lower elevations. Moreover, areas at low elevations are drier because there is less precipitation, with higher temperatures and evaporation over summer (Mark 1965d, Maunder 1965).

Both elevation and rock type were correlated with several other measured environmental variables. Soil chemistry changed with elevation in the present study, which may be related to the observed changes in species richness. The different leaching properties of each rock type may also alter soil chemistry (McLaren and Cameron 1996), although this was not observed with the measured soil chemistry variables. The correlation between rock type and tenure may be explained by the clustering of transects in conservation tenure in geographic space (Figure 14). These complex interactions between environmental variables make it difficult to know which factors are actually causing the observed changes in species richness.

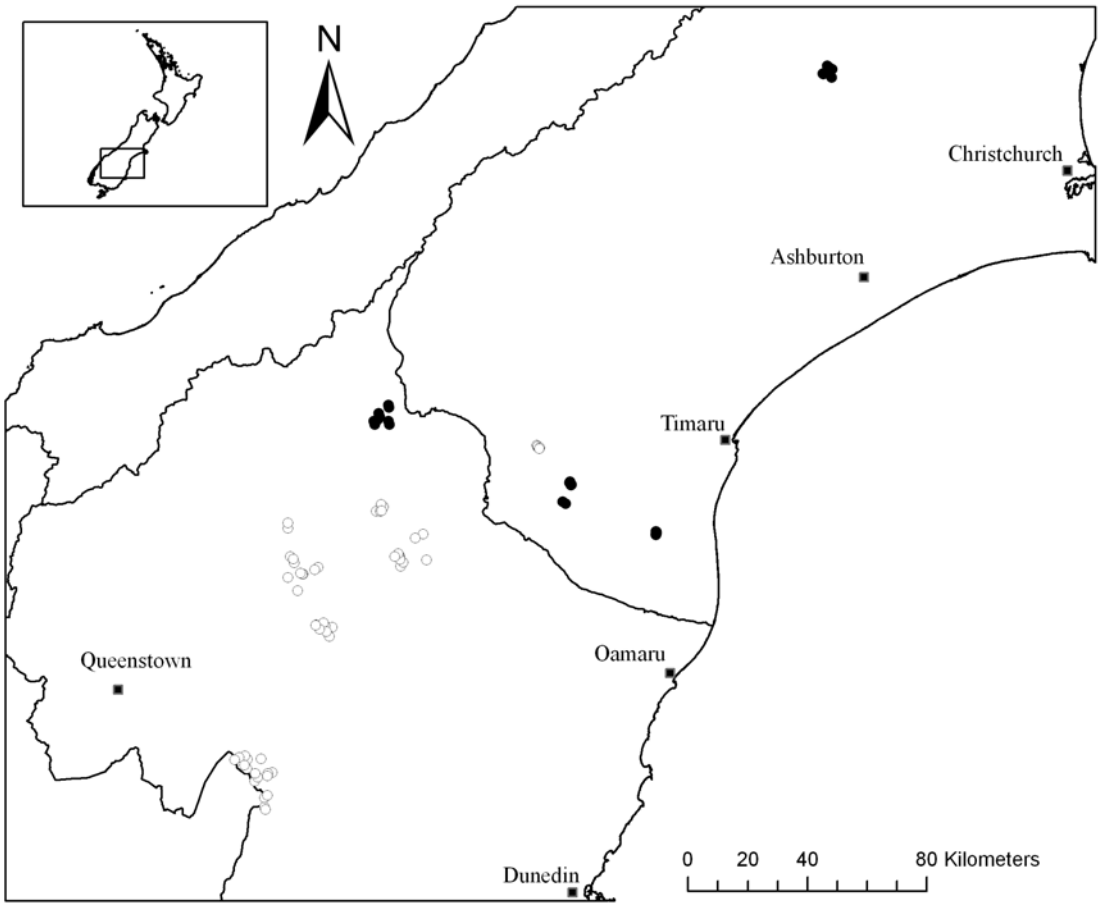

Figure 14: Location of 90 transects in tussock grasslands across Canterbury and Otago in different tenure categories. Filled circles represent 26 transects that were in pastoral tenure; open circles represent 64 transects that were in conservation tenure at the second measurement.

5.2. Explanations for changes in species richness

5.2.1. Sampling artefacts

Given that few studies have shown increases in species richness in tussock grasslands, it is appropriate to consider the likelihood that sampling artefacts were responsible for a "false increase" in species richness at the third measurement. In other words, misidentifying or inconsistently identifying plant species at any measurement time would lead to a different number of species being recorded as present. Species richness could be inflated at a given measurement time, for example, by incorrectly identifying one species as two separate species. Species richness could also be deflated at a given measurement time, for example, by identifying two separate species as one species. Consistency and accuracy in observers is critical in long-term monitoring, especially when identifying to the species level (Rose 2003, Eskelinen and Oksanen 2006). Misidentifications or inconsistent identifications are unlikely to have occurred in the present study, as the same botanist was involved in species identification at each measurement time. However, if plant species had been misidentified, this would have been consistent across measurements, which makes the results comparable over time. Furthermore, the ten transects that were re-measured independently of the field team by C. Jensen in 2005 also showed an increase in mean quadrat species richness at the third measurement, which shows that these patterns are consistent.

Given that alpine plants only flower for short periods (Mark 1965b, Wardle 1978) and that flowers are critical for correctly identifying many grasses and small herbs to species level, the seasonal consistency of measuring times is important for the comparison of plant communities across years (Small and McCarthy 2002). In the present study all of the transects were re-measured at the same time of year that they had been established and/or measured previously (November-March). As much as possible, transects were re-measured during the same month that they had been established and measured previously. Not only does this further mitigate the chances of incorrectly inflating or deflating species numbers, it means that species will always be identified by the same characteristics, and the probability of detecting differences between species should stay relatively constant. These methods ensured that sampling artefacts were unlikely to be responsible for the observed changes in species richness.

5.2.2. Changes in exotic species richness

Changes in vegetation in tussock grasslands are often presented to be driven by exotic species (Rose et al. 1995, Walker 2000, Meurk et al. 2002, Rose et al. 2004, Espie and Barratt 2006). For example, exotic species have been found to increase at the expense of native species in the Harper-Avoca valley, on Flat Top Hill, and in the Mackenzie Country (Rose et al. 1995, Walker 2000, Meurk et al. 2002). However, the changes in species richness seen in this study are not directly attributable to changes in exotic species richness. In fact, although species richness increased during the second time interval, exotic species richness did not increase significantly at either the quadrat or the transect scale (Tables 3 and 8, Figure 8). Nearly 50% of exotic species on these transects are annuals (33 out of 68). Considering that each transect was measured on one day of the year, the presence of some of these short-lived exotic annual species may not have been detected. However, the transects were always remeasured at the same time of year, which avoids this effect as much as was possible.

Often, the studies that attribute vegetation changes in tussock grasslands to exotic species are geographically restricted, in that they are located within one reserve (e.g. Walker 2000, Mark and Dickinson 2003) or catchment (e.g. Rose et al. 1995, Rose et al. 2004). This means that environmental variables such as soil type and climate are similar, and may have been optimal for exotic species to dominate vegetation change. Perhaps exotic species are important drivers of changes in species richness under certain environmental conditions. For example, Walker (2000) found that exotic species were important drivers of changes in species richness at low elevations between 300 and 545 m. Overall, changes in species richness over the wide elevational range in the present study were not driven by exotic species.

5.2.3. Tenure differences

The only significant increase in mean quadrat exotic species richness occurred on conservation land during the second time interval (Table 5), which could be because they have increased competitive ability with populations that are no longer suppressed by herbivory (Norton 1988, Meurk et al. 1989, Lord 1990, Walker 2000). However, native species richness increased during the second time interval on both conservation and pastoral tenure. This contrasts with the findings of Walker (2000), which showed that exotic species richness increased at the expense of native species richness where grazing had ceased. In addition, Rose et al. (1995) found that native species declined and exotic species increased in both

grazed and ungrazed short-tussock grasslands. In the present study, tenure was used as a coarse measure of differences in grazing, and seems to have had no obvious effect on changes in native species richness, because they declined and then increased on both conservation and pastoral tenure.

Woody species can increase in the absence of grazing in tussock grasslands, which may eventually lead to the establishment of native woodlands (Meurk et al. 2002). This may be because in the absence of grazing in pre-human New Zealand there were patches of montane vegetation that were characterised by a mixture of grass and shrub species (McGlone 2001). The cessation of grazing may lead to vegetation with similar characteristics. In the present study, of the 88 transects that woody species were present on, transects in conservation tenure increased in mean quadrat woody species richness significantly more than transects in pastoral tenure (two-sample *t*-tests: first time interval: $t = 3.53$, d.f. = 86, $P = 0.001$, equal variances, second time interval: $t = 2.20$, d.f. = 86, $P = 0.030$, equal variances). This supports the idea that removing grazing will result in a reversion of tussock grasslands to a grassland-shrubland mosaic (Meurk et al. 2002).

Overall, mean quadrat species richness decreased between the first and second measurements and then increased between the second and third measurements, regardless of whether the land was in conservation or pastoral tenure (Table 4, Figure 9). Also, tenure was not a significant predictor of species richness change for either period (Table 7). This contrasts with other studies, where changes in vegetation in tussock grasslands has been considered to be primarily driven by factors relating to management (e.g., Treskonova 1991, Walker 2000, Rose et al. 2004). However, the transects in conservation tenure were spatially clustered which may have influenced the analyses by not being independent, i.e. they may have been spatially autocorrelated (Figure 14). It is important to note that within each tenure category, areas are managed differently depending on the environment. For example, within pastoral tenure, land at different elevations is managed differently. High elevation areas may be seldom grazed, and fertiliser rarely applied (lessees, personal communication 2005-2007; names with-held for confidentiality). By classifying areas by tenure, we neglect to take these more subtle differences into account, which could explain why tenure was not a significant predictor of change in mean quadrat species richness. In addition, the effects of management on vegetation change will also differ according to the environment (Rose et al. 1995) and the only way to attribute management practices to vegetation change in tussock grasslands is if

the management history of the area is known (Diaz et al. 1994), which it was not for this study.

5.2.4. Changes in rabbit densities throughout the time period

Changes in rabbit densities over the last 24 years may have influenced changes in plant species richness on the transects in the present study. However, without exclosure plots near the transects measured this is only speculation. Species richness declined during a period when rabbit numbers were high in the 1990s, and species richness increased during a period when rabbit numbers were low in the 2000s (Figure 15). Browsing by rabbits depletes vegetation, reduces biomass, and may lead to patches of exotic species in New Zealand's tussock grasslands (Petrie 1883, Cockayne 1920, Connor 1964, O'Connor 1981, Norbury and Norbury 1996, Norbury et al. 2002). Species richness may be expected to decline due to rabbit browsing, because they create large bare patches of ground, allowing competitively dominant species to become abundant, and are selective in the plant species that they eat (Connor 1964, Norbury and Norbury 1996, Reddiex 1998). Changes in species richness on these 90 transects in tussock grasslands may be related to changes in rabbit populations during this period, but this is difficult to prove.

5.2.5. Changes in precipitation

In semi-arid environments such as the Canterbury and Otago high country, precipitation events are important for determining vegetation patterns and vegetation change (Grant and French 1990, Walker 1997, Wiegand and Jeltsch 2000, D'Odorico et al. 2005, Hereford et al. 2006, Potts et al. 2006). Walker (2000) partially attributed the increase in species richness to high rainfall over the four years of her study. It could be thought that in the present study, the increase in species richness at the third measurement was due to high precipitation during 2004 and 2005. However, rainfall data from Lake Tekapo, which is roughly at the geographic centre of the transect locations, does not support this hypothesis. Mean annual rainfall at Lake Tekapo was high in the mid-1990s when species richness decreased, but relatively low in 2004 and 2005 when species richness increased (Figure 16). Therefore, mean annual rainfall does not appear to explain the observed changes in mean quadrat species richness in the present study. Recent work suggests that fluctuations in precipitation are more important drivers of species richness than the amount of precipitation in dryland ecosystems (D'Odorico et al. 2005, Adler and Levine 2007). Precipitation events may be influencing the observed changes in species richness seen in the present study, but in a way that is unclear.

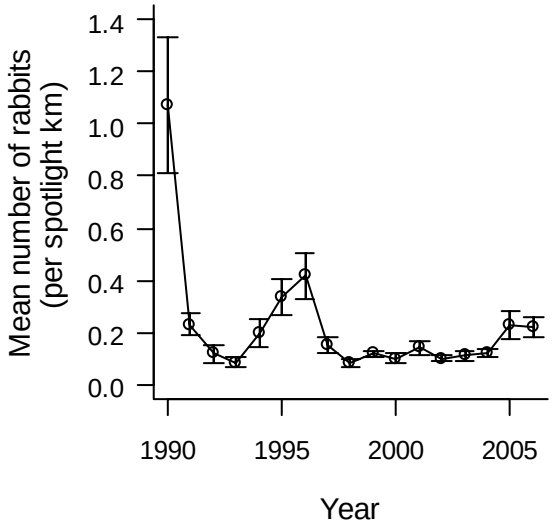

Figure 15: Densities of rabbits in the South Island high country in the South Island of New Zealand, measured by spotlight counts. The data here show 642.6 km of spotlight transects in the Mackenzie Country, Omarama and Kurow, which were measured annually during spring. Data obtained from Environment Canterbury.

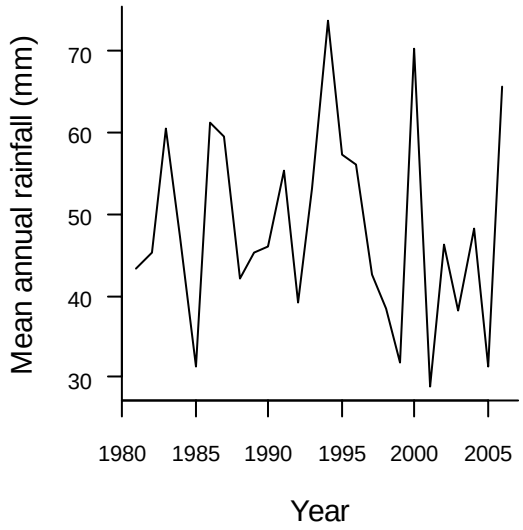

Figure 16: Mean annual rainfall (mm) between 1981 and 2006 at Mt Hay Station, Tekapo. Data obtained from cliflo database, NIWA.

6. Conclusions

There has been a geographically widespread decline and then increase in species richness in South Island tussock grasslands over the past 24 years. Small herb species and native species were important drivers of these changes, because they varied in small and large scale species richness at each measurement. This could be because they are an inherently variable group, or because they are vulnerable to the processes that are driving this geographically widespread pattern. There is an interaction between elevation and the processes that are driving changes in species richness, which may be related to climate or soil chemistry. Traditional explanations given for changes in species richness in tussock grasslands are the effects of exotic species and tenure differences (Dickinson et al. 1992, Rose and Platt 1992, Walker 2000, Meurk et al. 2002). Neither of these hypotheses account for the changes in species richness observed on these 90 transects, indicating that a shift in our focus on the causes of vegetation change in tussock grasslands may be required if we are to understand the complex patterns observed.

Chapter 3: Spatial and Temporal Attributes of Species Composition in Tussock Grasslands

1. Abstract

New Zealand's South Island tussock grasslands are highly modified, largely due to agricultural development, introduced pests, and invasion by exotic weeds. As part of the Tenure Review process, many areas have recently been retired from grazing. This is likely to result in significant changes in the vegetation; however, what these changes will be is unclear. This research investigated changes in tussock grassland vascular plant communities that have occurred since the 1980's in Otago and Canterbury. Data collected from 90 permanently marked transects were used to assess spatial and temporal changes in plant species composition. Transects represented land in both conservation and pastoral tenure. A cluster analysis (two-way indicator species analysis: TWINSPAN) identified four compositionally different communities present in these 90 transects, which were strongly related to elevation. A refined data set, containing only transects that represented short- and tall-tussock grassland communities, was analysed using ordination (detrended correspondence analysis). Change in composition over time was weakly related to solar radiation, the property a transect was located on, or whether it was in a short- or tall-tussock grassland community. Changes in composition were not related to tenure. These results indicate that changes in plant species composition in the South Island's tussock grasslands are complex and unpredictable at the spatial and temporal scales examined.

2. Introduction

Many studies recognise distinct vascular plant community types within tussock grasslands and that the occurrence of these communities is strongly correlated with environmental variables (Hubbard and Wilson 1988, Partridge et al. 1991, Walker et al. 1995, Walker et al. 1999, Walker 2000, Meurk et al. 2002). For example, Norton et al. (2006) showed a relationship between soil fertility and species composition in the Mackenzie Basin, and Wilson (1989) showed that the distributions of native and exotic species in the Upper Clutha were primarily related to elevation. These results are often based on measurements at one place and at one time (i.e. "snapshot" studies) making it difficult to determine how strong these trends are over larger environmental gradients. Encompassing tussock grasslands from a

broad geographic area, and over a long time period, will allow us to gain a better understanding of the changes in species composition that can occur in both space and time.

Few long-term studies (10+ years) exist for South Island tussock grasslands (e.g., Treskonova 1991, Rose et al. 1995, Mark and Dickinson 2003, Rose et al. 2004). Investigations of temporal changes in tussock grasslands generally focus on changes that occur after grazing removal, with particular emphasis on changes in *Chionochloa* and the invasive exotic *Hieracium* species (Allen 1993, Rose et al. 1995, Hunter and Scott 1997, Meurk et al. 2002, Mark and Dickinson 2003, Rose et al. 2004). Some of these studies show that tussock grasslands have become dominated by exotic species over time, even after grazing has been removed (Allen et al. 1995, Rose et al. 1995, Hunter and Scott 1997, Grove et al. 2002, Rose et al. 2004). Grazing, a key driver of vegetation change in tussock grasslands, influences annual changes in species composition (Allen et al. 1995). We would therefore expect that changes in tussock grassland plant species composition would differ according to whether they are in conservation or pastoral tenure.

Tussock grasslands throughout the South Island are highly modified, largely due to increased fire frequency, agricultural development, introduced pests and herbivores, and invasion by exotic weeds (Mark 1993). This means that changes in composition that occur after these influences are removed are largely unpredictable (Grove et al. 2002). Understanding how environmental variables relate to species composition in tussock grasslands may allow us to understand how influential management practices have been in shaping the current patterns that we see.

This chapter investigates the spatial and temporal patterns in plant community composition that occurred in tussock grasslands by using 24 years of data from 90 permanently-marked transects in tussock grasslands throughout Canterbury and Otago. Specifically, I will ask: (1) What are the distinct vascular plant community types in these tussock grasslands? (2) What are the main gradients in species composition, and how are they related to environmental variables? (3) How has species composition changed over time, and are these changes related to tenure?

3. Methods

Study area and data collection are described in Chapter 2, sections 2.1 and 2.2.

3.1. Data analysis

To reduce the variation in the full data set (90 transects, 347 species), all analyses included only species that were present on at least two transects for at least two measurements (90 transects, 265 species). Species' abundances were calculated by summing the number of quadrats that each species occurred in on each transect, which were used in the two-way indicator species analysis (TWINSPAN) and ordinations.

3.1.1. Analysis of spatial patterns

To investigate how species composition may vary in space, species and transects were classified into relatively homogeneous plant communities using two-way indicator species analysis (TWINSPAN, Hill et al. 1975, Gauch 1982, Leps and Smilauer 2003), implemented in PC-ORD version 4 (McCune and Mefford 1999). TWINSPAN was chosen because it is a robust and effective clustering method with most data (Gauch 1982, Minchin 1987), and has successfully classified tussock grasslands into ecologically meaningful communities in the past (Hubbard and Wilson 1988, Partridge et al. 1991, Walker et al. 1995, Walker et al. 1999). The TWINSPAN was performed on abundance data from all 90 transects from the three measurements (270 transects, 265 species).

The gradient structure of plant community composition and the environment was investigated using ordination. Ordinations organise species, samples and environmental variables along axes. The importance of each axes in explaining the variation in species composition is given by eigenvalues (Leps and Smilauer 2003). Gradient lengths express species turnover along the axis, and are given in standard deviation units (ter Braak and Smilauer 2002). Indirect ordination, by detrended correspondence analysis (DCA), was used to infer which of the measured environmental variables correlated with variation in species composition (Leps and Smilauer 2003). DCA was used because it is visually easy to interpret and gives a measure of species turnover in space. DCA has also been used extensively in tussock grassland research (e.g. Hubbard and Wilson 1988, Partridge et al. 1991, Allen et al. 1995, Walker et al. 1995, Gibson and Bosch 1996, Allen et al. 1997, Walker et al. 1999). Data from all 90 transects at the three measurements were used in the DCA, with detrending by 26 segments. Six

environmental variables were overlaid on to the ordination to examine correlations with the species data; these were the same variables that were used in the changes in species richness models: elevation, rock type, soil type, tenure, burning occurrence between the first and second measurements, and solar radiation (Table 2).

A second DCA was performed using a reduced dataset containing only transects that were classified as either short- or tall-tussock grassland communities (see Results) by the TWINSPAN. This dataset contained 207 species on 53 transects at the three measurements. Transects in the short- and tall-tussock grassland communities ranged in elevation from 648 m to 1560 m and covered a wide geographic area (Figure 17). Of the 53 transects, 23 transects were in conservation tenure, and 30 transects were in pastoral tenure (at the second measurement). All remaining analyses were performed using only the short- and tall-tussock grassland TWINSPAN communities.

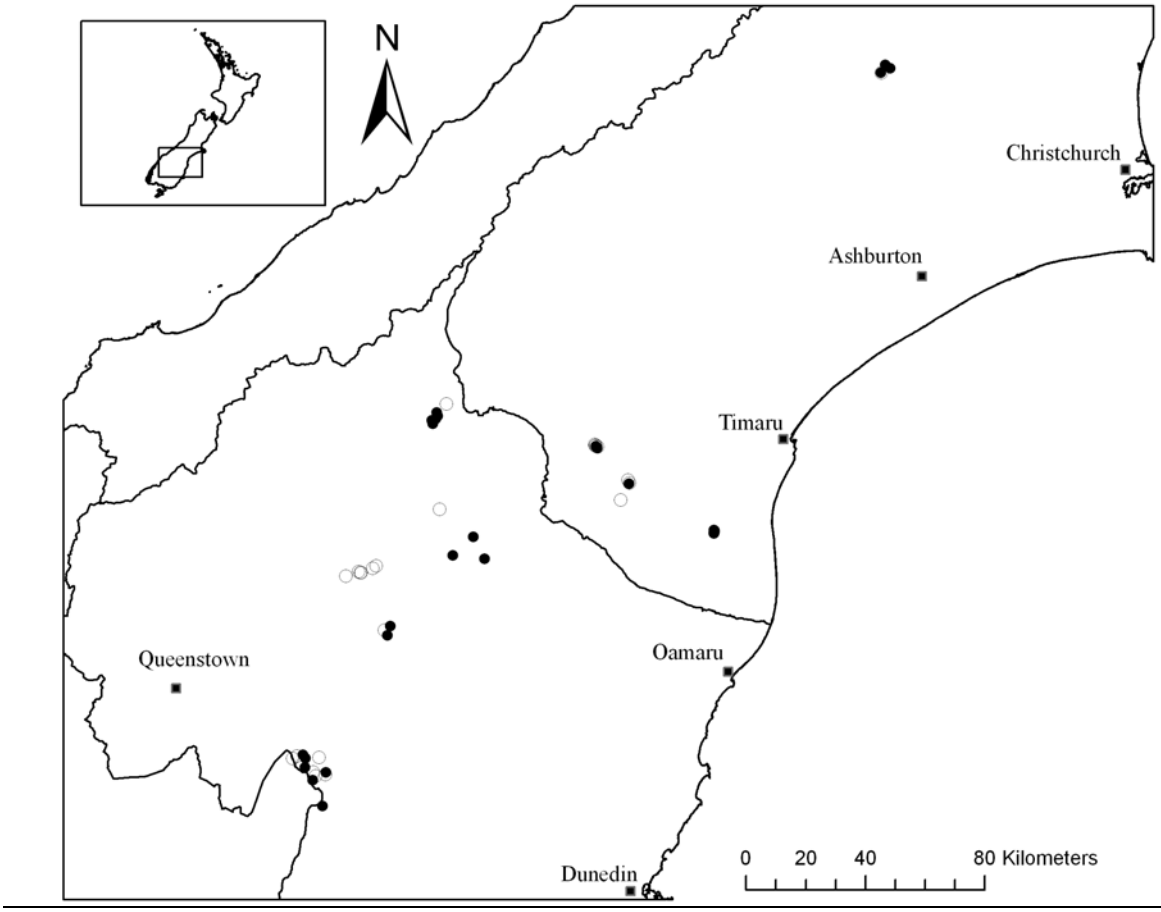

Figure 17: Location of 53 transects in short- and tall-tussock grassland TWINSPAN communities across Canterbury and Otago. Filled circles represent tall-tussock grasslands, open circles represent short-tussock grasslands.

CCA constrained the ordination axes so that they had a direct linear relationship with the environmental variables measured (Leps and Smilauer 2003). A separate CCA was performed for each measurement to investigate the spatial patterns in species composition, and assess the importance of each environmental variable at each measurement. CCA was used because it performs well if there is more than one gradient driving species composition (Palmer 1993). To account for spatial autocorrelation on transects clustered within properties, property was put in to the CCA as a covariable. Environmental variables used to constrain the ordination axes were elevation, solar radiation, tenure, soil type, burning between the first and second measurements, log soil phosphorus, and log soil sodium. Other soil variables were correlated with elevation (Table 6). Rock type was not included because it was correlated with the property covariable. Forward selection was used to look for environmental variables that were significant for explaining variation in species composition, with Monte Carlo permutation tests (499 permutations, $P < 0.05$). For each measurement, the CCA was then run including only those environmental variables that were significant, and the significance of the axes were tested. All ordinations were performed in CANOCO version 4.5 (ter Braak and Smilauer 2002).

3.1.2. Analysis of temporal patterns

Changes in composition over time were displayed on a DCA diagram by plotting trajectories of each transect between the first and second measurements (first time interval), and between the second and third measurements (second time interval). This method has been used previously to investigate changes in composition over time (e.g., Collins and Adams 1983, Leps 1987, Kahmen et al. 2002, Meurk et al. 2002). The distance between points on each transect was used as a measure of the amount of compositional change that has occurred between measurements. For each transect, the Euclidean distance between points on the DCA graph at each measurement was calculated using Pythagoras' theorem. The distance between two points on the graph was treated as the hypotenuse of a right-angled triangle. The lengths of the sides of the triangle were calculated as the distance between each measurement on the first axis and the second axis respectively (Equation 1).

$$D = \sqrt{d_1^2 + d_2^2}$$

Equation 1

For the first time period, d_n is the distance between the first and second measurements on DCA axis *n*. Similarly, for the second time period, d_n is the distance between the second and third measurements on DCA axis *n*. Separate analysis of variance tests (ANOVAs) were used to test if the distance moved by a transect was related to measured environmental factors: property, tenure, TWINSPAN community, rock type, soil type or burning. Linear regressions tested for relationships between the distance moved and continuous environmental variables: elevation or solar radiation.

A direction category for each transect, describing how each transect had changed in composition during the first time interval, and then during the second time interval, was generated by classifying the direction of change on the DCA graph into one of four categories: (1) moved negatively on the first axis and positively on the second axis, (2) moved positively on the first axis and positively on the second axis, (3) moved negatively on the first axis and negatively on the second axis, (4) moved positively on the first axis and negatively on the second axis. Chi-square tests for goodness of fit (Zar 1999) were performed to investigate whether the direction of change was related to measured environmental factors: property, tenure, TWINSPAN community, rock type, soil type or burning. Because there were low sample sizes in some categories, *P* values were estimated by Monte Carlo simulations based on 2000 replicates (Gotelli and Ellison 2004). Generalised linear models, using the Poisson link, tested for relationships between the direction moved and continuous environmental variables: elevation or solar radiation. All temporal analyses were performed in R version 2.5.1 (R Core Development Team 2007).

4. Results

4.1. Spatial patterns in species composition: 90 transects

4.1.1. TWINSPAN community groups

Inspection of the TWINSPAN diagrams led to stopping at four community groups that were the best for showing major site and species groups (Figure 18). The first division for the community groups distinguished transects where *Chionochloa* species were abundant from those where it was not. The second division distinguished transects with abundant alpine species, such as *Agrostis muelleriana*, from those that did not. The third division identified transects where *Gaultheria depressa* was abundant. The fourth division distinguished

transects that contained *Festuca novae-zelandiae*, *Discaria toumatou* or *Linum catharticum*, from those that did not. Each TWINSPAN community differed in mean elevation (Figure 19), although those differences were not significant (ANOVA: $F_{1,\ 268} = 0.87$, $P = 0.351$). A description of each community group follows.

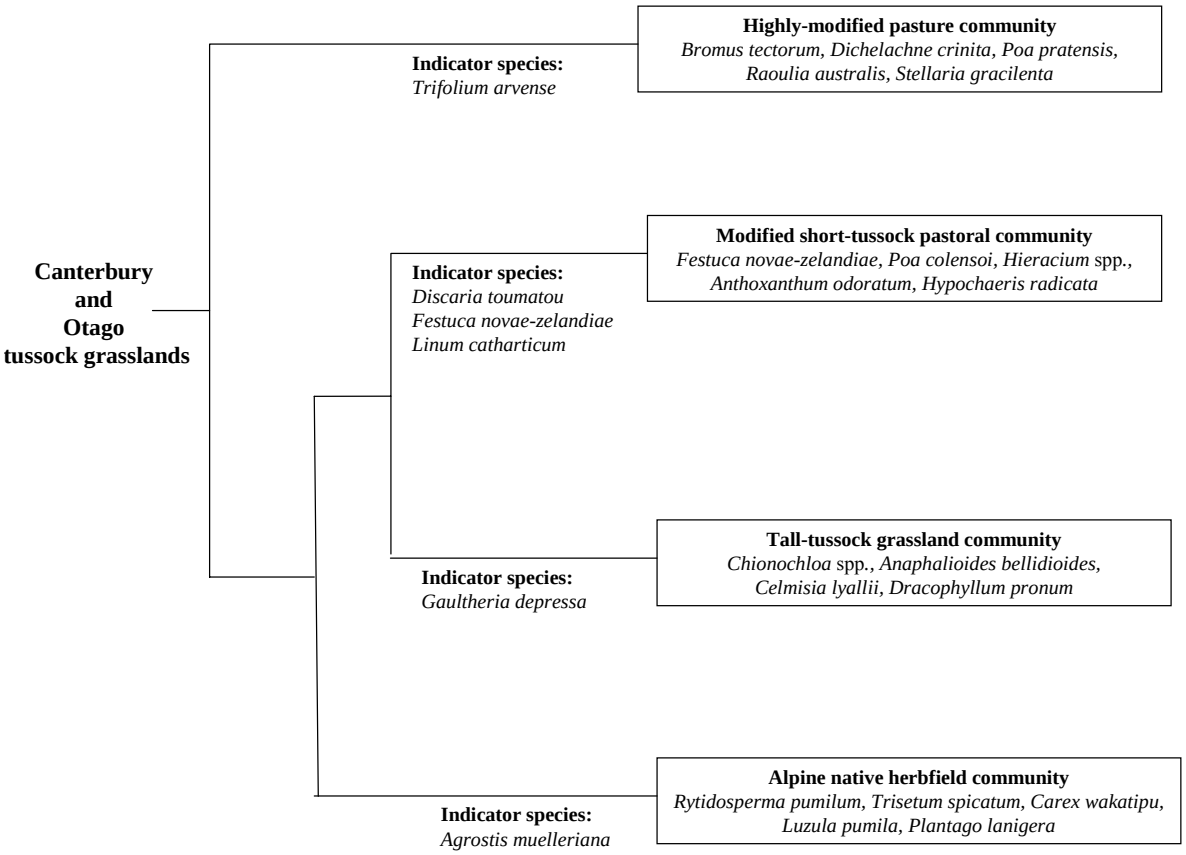

Figure 18: Diagram of the four distinct vegetation groups that were identified by the TWINSPAN, showing indicator species and typical species for each group. The analysis was performed with 265 species that occurred on 90 transects at the three measurements.

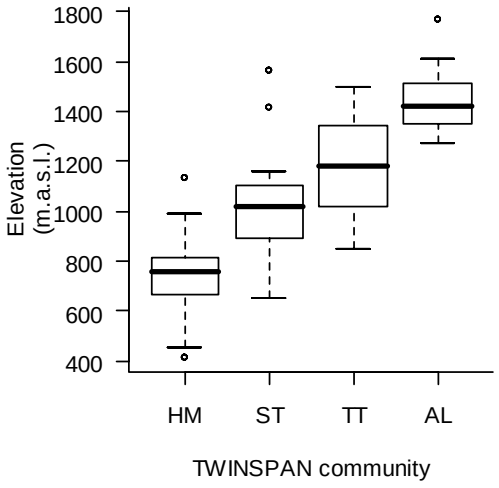

Figure 19: Boxplot showing relationship between TWINSPAN community and elevation. The median elevation for each community is the dark line, the upper and lower quartiles are represented by the outer ranges of the boxes, the upper and lower extremes are represented by the horizontal lines. The points represent outlying values for each community. HM = highly-modified pasture community, ST = short-tussock grassland community, TT = tall-tussock grassland community, AL = alpine mat-forming species community.

Table 9: Results from detrended correspondence analysis for 265 species on 90 transects at three measurements in tussock grasslands throughout Canterbury and Otago. See text for definitions of terms.

Properties: DCA	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues	0.66	0.42	0.28	0.22
Lengths of gradient	6.03	4.41	4.06	2.57
Species-environment correlations	0.94	0.61	0.59	0.45
Cumulative percentage variance:				
Of species data	7.5	12.3	15.6	18.2
Of species-environment relation	28.0	34.3	0.0	0.0
Sum of all eigenvalues (total inertia)	8.71			
Sum of all canonical eigenvalues	1.12			

Community one: Highly-modified pasture communities.

Indicator species: Trifolium arvense

These highly-modified transects where *Chionochloa* species were not present ranged in elevation from 400 to 1000 m, and were all in pastoral tenure. This community contained the highest proportion of exotic species (59%), with herbs such as *Erodium cicutarium* and *Echium vulgare*, and the grasses *Dactylis glomerata, Bromus tectorum* and *Vulpia bromoides*. Most transects in this community were on north-facing aspects and had high solar radiation indices. This accounted for annual species, such as *Trifolium dubium, Verbascum thapsus* and *Spergularia rubra,* making up 44% of all species in the community. Native species in this group were low-growing, including *Raoulia australis, Raoulia beauverdii, Poa maniototo* and *Oxalis exilis.*

Community two: Modified short-tussock grassland communities.

Indicator species: Discaria toumatou, Festuca novae-zelandiae, Linum catharticum

The modified short-tussock grassland community contained transects that were between 600 and 1400 m in elevation. Many transects had been burned between the first and second measurements (26%) and most were in pastoral tenure (74%). Two prominent native tussock species, *Festuca novae-zelandiae* (short-tussock) and *Poa colensoi* occurred in this community. Exotic species made up 34% of species in this community, including the three most abundant *Hieracium* species in the data set (*H. pilosella, H. lepidulum* and *H. praeltum*) and the exotic grasses *Holcus lanatus* and *Anthoxanthum odoratum.* There were also exotic herbs including *Hypochaeris radicata, Cerastium fontanum,* and *Linum catharticum* and native woody species such as *Muehlenbeckia axillaris, Discaria toumatou,* and *Coprosma atropurpurea*. There were fewer annual species (18%) than in the highly modified pasture community.

Community three: Tall-tussock grassland communities.

Indicator species: Gaultheria depressa

Transects in the tall tussock grassland community were between 900 and 1500 m in elevation, and most were on conservation tenure (78%). Neither exotic nor annual species were strongly

associated with this community. The tall-tussock community was characterised by *Chionochloa* spp. and intertussock herbs such as *Anaphaloides bellidioides, Celmisia spectabilis*, *Brachyglottis bellidioides* and the low-growing fern *Blechnum penna-marina*. Woody species in this community included *Gaultheria depressa, Dracophyllum uniflorum, D. pronum* and *D. acerosum.*

Community four: Alpine mat-forming species community communities.

***Indicator species:* Agrostis muelleriana**

At 1300-1800 m, transects in the alpine mat-forming species community represented the highest elevations measured in the study and most were in pastoral tenure (84%). There were no exotic species associated with this community, which consisted of mainly low-lying perennial herbs including *Plantago lanigera*, *Celmisia laricifolia*, and *Euphrasia zelandica*, and mat-forming species such as *Chionohebe densifolia, Raoulia hectorii* and *Hectorella caespitosa.* Species characteristic of wet soils, including *Abrotanella inconspicua* and *Gnaphalium mackayii* were also present in this community.

4.1.2. Unconstrained ordination

The large degree of variation in species composition reflected by the separation of the TWINSPAN communities was reinforced in the DCA results for all 90 transects. Total inertia, a measure of the amount of variance in the species composition data, was high, at 8.71 (ter Braak and Smilauer 2002, Table 9). Eigenvalues measure the importance of each axis for describing the variation in species composition (ter Braak and Smilauer 2002). The high eigenvalues for the first and second axes, and the much lower eigenvalues for the third and fourth axes, indicates that there were two strong gradients in species composition (Table 9). An axis with a gradient length of 4 standard deviations means that there has been one full turnover in species composition on the axis, i.e. species at one end of the axis were not present at the other end of the axis (Kent and Coker 1992). There was high turnover on both the first and second axes (Table 9). These two axes explained only 12.3% of the total variance in the species data (ter Braak and Smilauer 2002, Table 9). Of the variation in the data that could be explained, the cumulative percentage variance of the species-environment relation shows that the first and second axes explained 34.3% (ter Braak and Smilauer 2002, Table 9).

The first gradient in species composition was strongly correlated with elevation and negatively correlated with soil type and solar radiation (Table 10). Tenure and rock type were weakly negatively correlated with the second axis, although they were also related to each other; transects in conservation tenure only occurred on greywacke rock. Transects in conservation tenure had a relatively narrow range of composition compared to transects in pastoral tenure (Figure 20). Some transects in pastoral tenure were similar in species composition to those in conservation tenure. Scatterplots for both the sites and species DCA scores took on a trumpet-like shape, because of extreme scores in transects on the second axis (Figures 20, 21 and 22). Extreme transects at the positive end of the first axis and had high values on the second axis were located near swampy areas. Those transects at the positive end of the first axis and had low values on the second axis were on exposed flat ridges. Kent and Coker (1992) suggest removing sites with extreme values to avoid outlying sites driving the DCA. When the transect with the most extreme value was removed from the data set, and the DCA was re-run, the graph continued to show these characteristics. This shape is therefore likely to be an artefact of a long compositional gradient.

TWINSPAN communities were well-separated along the first DCA axis, which was correlated with elevation (Table 10, Figure 21). Exotic species were more abundant at lower elevations (Figure 22). Annual and exotic species, such as *Echium vulgare* and *Bromus tectorum*, were at the lowest elevations. Native species were more abundant at high elevations, and the highest elevations contained alpine species such as *Dracophyllum muscoides* and *Luzula pumila*. The invasive exotic species *Hieracium lepidulum, H. pilosella* and *H. praeltum* were at the highest elevations for exotic species, indicating that they may be able to increase their range in elevation further than other exotic species. *Chionochloa* spp. were abundant at higher elevations, and were weakly associated with transects in conservation tenure. *Festuca novae-zelandiae* was abundant in relatively low elevation areas compared to other native species, and *Poa colensoi* was associated with higher elevations and pastoral tenure (Figures 20 and 21).

Table 10: Correlations between environmental variables and detrended correspondence analysis axes at all measurements for 90 transects, and for 53 transects that were in the short- and tall-tussock grassland communities.

	All community groups (N = 90)		Short- and tall-tussock grassland communities (N = 53)	
Correlations: DCA	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
Elevation	0.81	-0.26	0.56	-0.53
Soil type	-0.63	-0.01	-0.19	-0.16
Solar radiation	-0.42	0.04	-0.39	-0.07
Tenure	-0.18	-0.40	-0.31	-0.46
Burnt	-0.07	0.05	-0.35	-0.24
Rock type	-0.04	-0.34	-0.30	-0.47

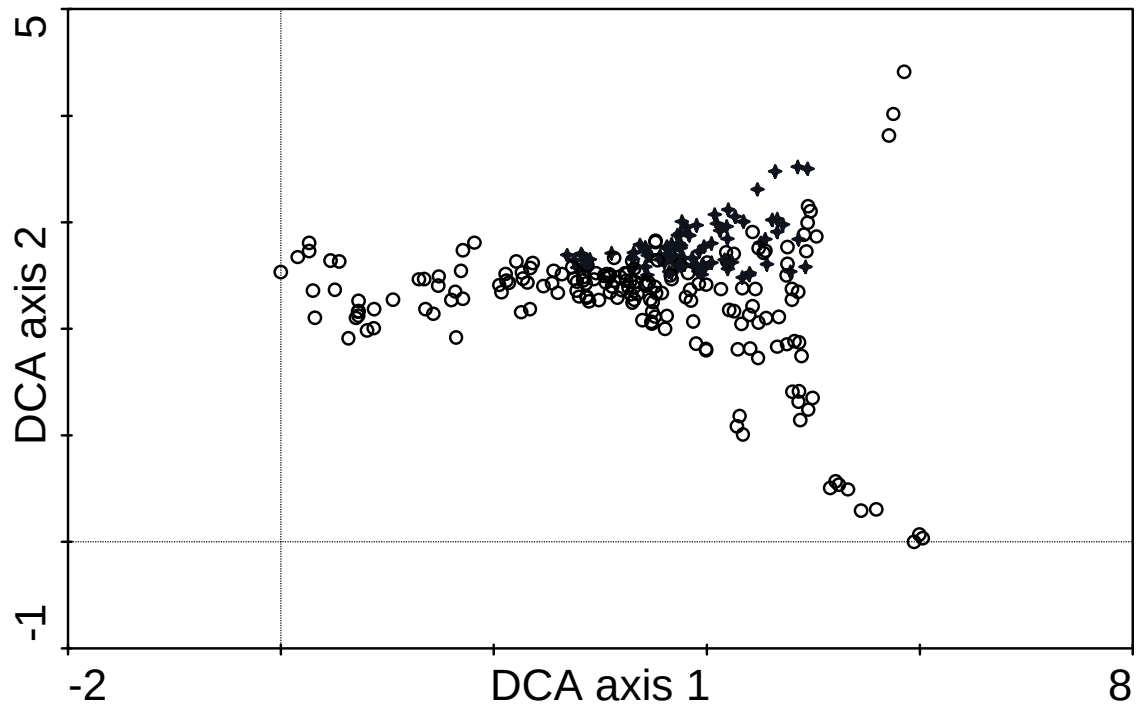

Figure 20: Scatterplot showing site scores from a detrended correspondence analysis of 265 species that occurred on 90 transects at three measurements in tussock grasslands throughout Canterbury and Otago, showing tenure categories. Filled stars represent transects in conservation tenure, open circles represent transects in pastoral tenure.

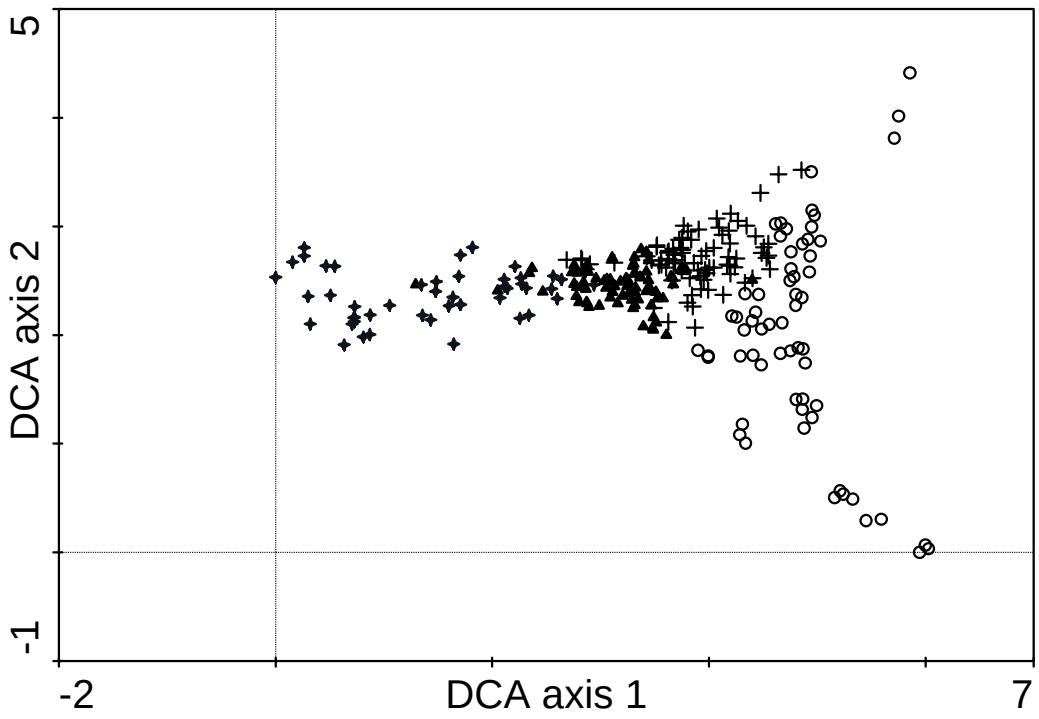

Figure 21: Scatterplot showing site scores from a detrended correspondence analysis of 265 species that occurred on 90 transects at three measurements in tussock grasslands throughout Canterbury and Otago, showing TWINSPAN communities. Filled stars represent the highly-modified community, filled triangles represent the short-tussock grassland community, plus-signs represent the tall-tussock grassland community, open circles represent the high alpine native community.

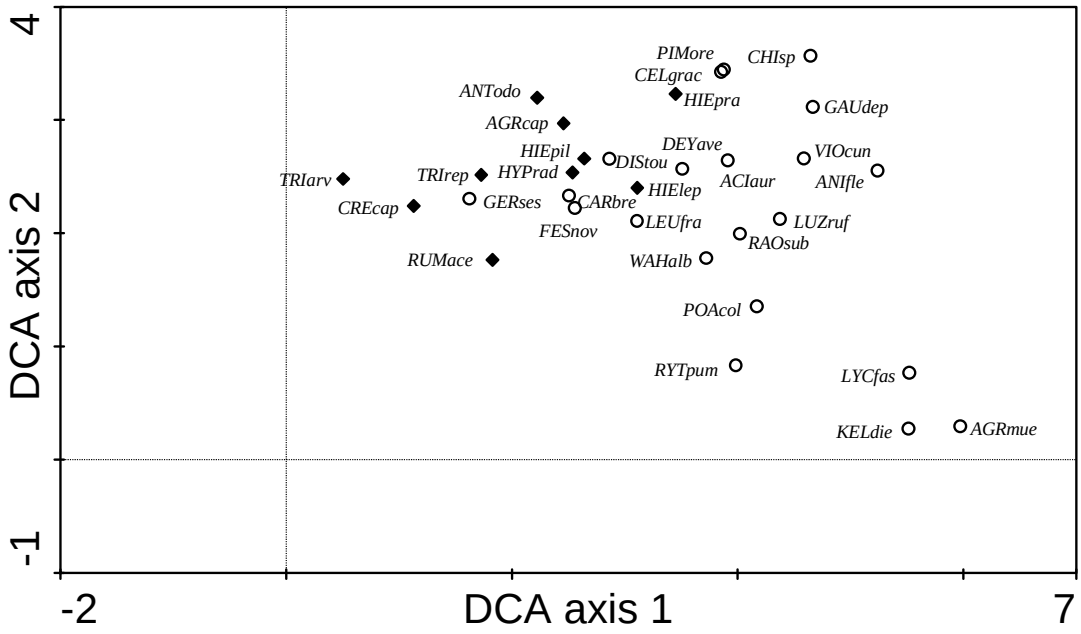

Figure 22: Scatterplot showing species scores from a detrended correspondence analysis of 265 species that occurred on 90 transects at three measurements in tussock grasslands throughout Canterbury and Otago. For clarity, only species with weights greater than 10% are shown. Filled diamonds represent exotic species, open circles represent native species. For definitions of species codes see Appendix I.

4.2. Spatial patterns in species composition: short- and tall-tussock grassland communities (n=53)

4.2.1. Unconstrained ordination

Variation in species composition was reduced by using the subset of transects that represented only short- and tall-tussock grassland communities from the TWINSPAN communities. These communities were selected because they represent "true" tussock grassland communities in that they typically contained *Festuca novae-zelandiae*, *Poa colensoi* and/or *Chionochloa* spp. (Figure 18). Total inertia for the DCA of the short- and tall-tussock grasslands was reduced to 3.99, which means that retaining only these two communities was an effective way to reduce the variation in species composition (Tables 9 and 11). Analysing only short- and tall-tussock grassland communities reduced the gradient lengths by less than half, because the axes were no longer driven by the distributions and abundances of unusual sites and rare species. The high eigenvalue and relatively long gradient for the first axis indicates that a single gradient underlies species composition in these short- and tall-tussock grasslands (Table 11). The species-environment relation shows that the first and second axes explain 46.6% of the variation that can be explained, and the percentage variance of species data shows that these axes explain 12.6% of the variation in species composition (Table 11).

Correlations between the measured environmental variables and the species composition data were weak (Table 10, Figure 23). Elevation was important for driving patterns in species composition because the eigenvalue for the first axis was high, and both the first and second axes correlated best with elevation. Solar radiation was negatively correlated with the first DCA axis. Tenure and rock type were negatively correlated with the second axis, which were also related to each other; transects in conservation tenure only occurred on greywacke rock.

Table 11: Results from detrended correspondence analysis for 207 species that occurred on 53 transects at three measurements in short- and tall-tussock grasslands. See text for definitions of terms.

Properties: DCA	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.31	0.19	0.15	0.13
Lengths of gradient	2.98	1.94	1.95	2.04
Species-environment correlations	0.85	0.80	0.50	0.41
Cumulative percentage variance:				
Of species data	7.9	12.6	16.2	19.4
Of species-environment relation	30.4	46.6	0.0	0.0
Sum of all eigenvalues (total inertia)	3.99			
Sum of all canonical eigenvalues	0.73			

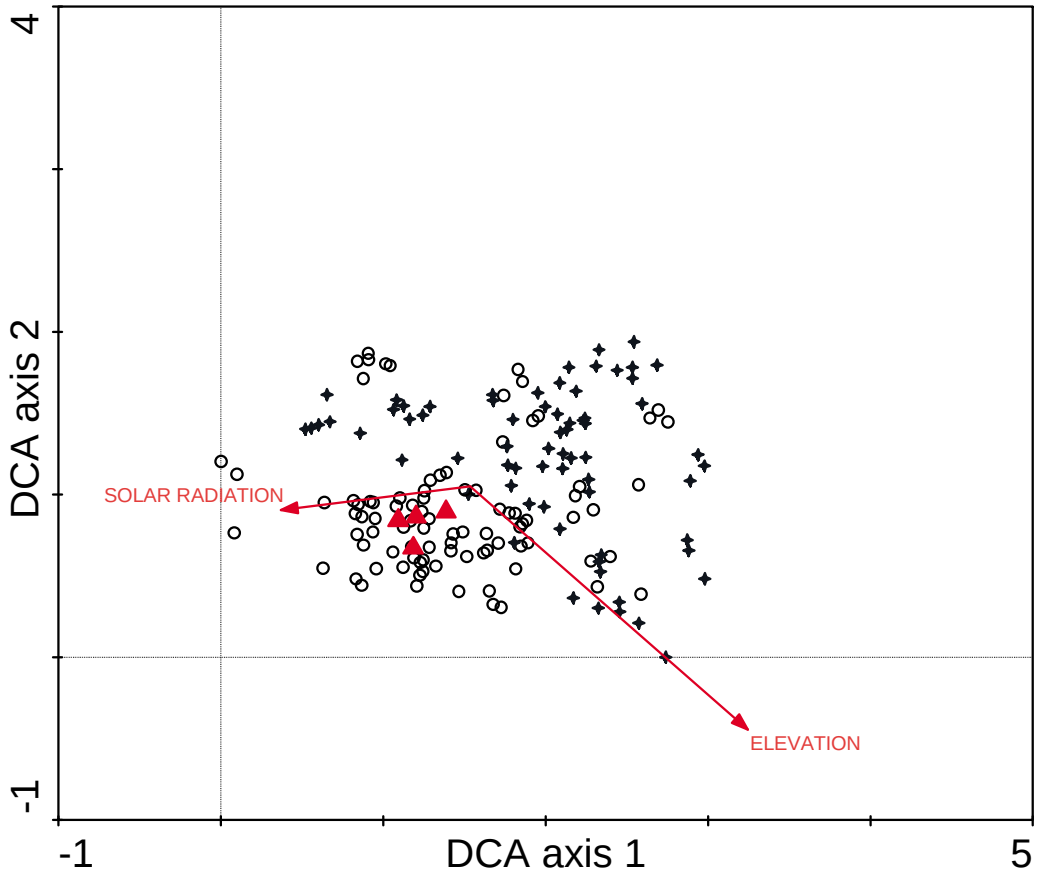

Figure 23: Scatterplot showing site scores from a detrended correspondence analysis of 207 species that occurred on 53 transects at three measurements in only the short- and tall-tussock grassland communities throughout Canterbury and Otago, showing tenure categories and environmental variables. Triangles represent categorical environmental variables, which are not labelled and are rock type, tenure, soil type and burning. Arrows represent continuous environmental variables. Filled stars represent transects in conservation tenure, open circles represent transects in pastoral tenure.

Exotic species were more abundant at low elevations (Figure 24). *Holcus lanatus* and *Trifolium repens* were abundant at low elevations in pastoral tenure, and both would have been oversown. The invasive exotic species *Hieracium pilosella* and *H. praeltum* were at the highest elevations for the exotic species and *H. lepidulum* was positively associated with pastoral tenure. Native species that were abundant in pastoral areas were low-growing, for example, the small herbs *Hydrocotyle novae-zelandiae* and *Leptinella pectinata*, and woody species such as *Carmichaelea vexillata* and *Pimelea oreophila*. There was broader representation of native species growth forms in conservation tenure, including large, species, such as *Dracophyllum uniflorum* and *Celmisia spectabilis*, as well as low-growing herbs such as *Lycopodium fastigiatum* and *Kelleria dieffenbachii*. *Festuca novae-zelandiae* was associated with pastoral tenure. *Chionochloa* was at mid-high elevations and was not strongly associated with either tenure category (Figures 23 and 24).

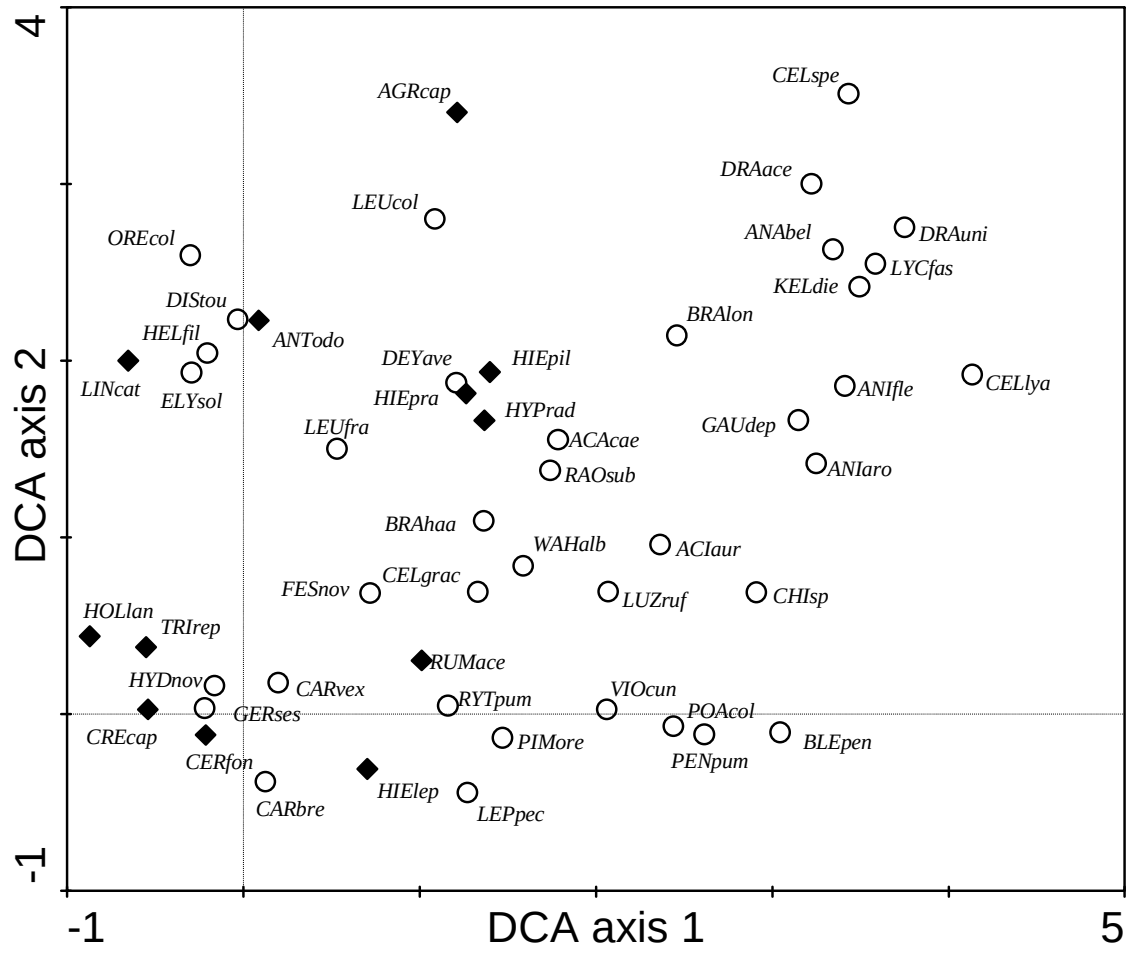

Figure 24: Scatterplot showing species scores from a DCA of 207 species that occurred on 53 transects at three measurements in only the short- and tall-tussock grassland communities throughout Canterbury and Otago. For clarity, only species with weights greater than 5% are shown. Filled diamonds represent exotic species, open circles represent native species. For definitions of species codes see Appendix I.

4.2.2. Constrained ordinations

Forward selection revealed that of the seven environmental variables put in to the CCA, only elevation and solar radiation influenced composition significantly at each measurement, after the variation explained by property had been accounted for (Table 12). Total inertia ranged between 3.28 at the first measurement, 3.30 at the second measurement, and 3.21 at the third measurement (Table 13). The species-environment correlations were high for the first and second axes for each CCA at each measurement, because the aim of CCA is to optimise this relationship (ter Braak 1987, ter Braak and Smilauer 2002). However, the sum of the canonical eigenvalues were low at each measurement, which shows that the there was a lot of unexplained variation in species composition that was not accounted for by elevation and solar radiation. The third and fourth axes were unconstrained because there were only two significant environmental predictors that could constrain the axes at each measurement. This can account for the relatively high eigenvalues for the third and fourth axes (Table 13). There was no relationship between tenure and species composition at any measurement.

Elevation was the strongest gradient by far, accounting for between 70 and 76% of the explainable variation at each measurement. Elevation was positively correlated with the first CCA axis at each measurement. Solar radiation was correlated with the second axis: positively at the first measurement, and negatively at the second and third measurements (Table 14 Figure 25). Both the first and second axes were significant at each measurement (Table 15).

Similar relationships between species composition and significant environmental variables were observed at each measurement. Species close together in ordination space have a similar distribution across transects (Gauch 1982, Leps and Smilauer 2003). While *Chionochloa* spp. and *Poa colensoi* were abundant at high elevations and associated with native species, *Festuca novae-zelandiae* was abundant at lower elevations and associated with both native and exotic species (Figure 26). This is because exotic species were most abundant at lower elevations. *Hieracium lepidulum*, *H. pilosella* and *H. praeltum* were all associated with *Festuca novae-zelandiae* at mid-low elevations (Figure 26). *Rumex acetosella* was at the upper limit of elevation for exotic species at each measurement. Native species abundant at lower elevations were generally low-growing, such as *Leucopogon fraseri*, *Helichrysum filicuale* and *Wahlenbergia albomarginata*. *Anisotome flexuosa* and *Gaultheria depressa* were abundant at high elevations and low solar radiation.

Table 12: Results of forward selection for canonical correspondence analysis for 53 transects in short- and tall-tussock grasslands at each measurement. Marginal effects show the variance in species composition that was explained by the variable alone. Conditional effects shows the extra variance in composition explained when each variable is added to the model sequentially, with associated *F*-statistics testing whether these variables explained a significant amount of variance, based on *P*-values from Monte Carlo tests. * *P* < 0.05, ns = not significant.

Variable	Marginal effects	Conditional effects	F statistic
First measurement			
Elevation	0.15	0.15	3.32 **
Solar radiation	0.10	0.10	2.30 **
Log (soil phosphorus)	0.05	0.05	1.23 ns
Log (soil sodium)	0.05	0.05	1.30 ns
Tenure	0.05	0.04	0.86 ns
Soil type	0.04	0.04	0.84 ns
Burnt between first and second measurements	0.02	0.02	0.48 ns
Second measurement			
Elevation	0.16	0.16	3.48 **
Solar radiation	0.09	0.10	2.17 **
Log (soil phosphorus)	0.06	0.06	1.23 ns
Log (soil sodium)	0.05	0.05	1.19 ns
Tenure	0.06	0.05	1.01 ns
Soil type	0.05	0.04	1.00 ns
Burnt between first and second measurements	0.03	0.04	0.90 ns
Third measurement			
Elevation	0.17	0.17	3.83 **
Solar radiation	0.08	0.09	1.95 **
Log (soil phosphorus)	0.06	0.06	1.35 ns
Log (soil sodium)	0.05	0.05	1.20 ns
Soil type	0.05	0.04	0.98 ns
Burnt between first and second measurements	0.04	0.05	0.93 ns
Tenure	0.04	0.03	0.80 ns

Table 13: Results from canonical correspondence analysis for 53 transects in Canterbury and Otago short- and tall-tussock grasslands at each measurement. Elevation and solar radiation were used to constrain the axes. First measurement: 162 species, second measurement: 164 species, third measurement: 165 species.

Properties: CCA	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
First measurement				
Eigenvalues	0.17	0.07	0.17	0.13
Species-environment correlations	0.91	0.91	0	0
Cumulative percentage variance:				
Of species data	9.00	12.80	21.60	28.30
Of species-environment relation	70.00	100.00	0	0
Total inertia	3.28			
Sum of all eigenvalues	1.93			
Sum of canonical eigenvalues	0.25			
Second measurement				
Eigenvalues	0.19	0.07	0.19	0.15
Species-environment correlations	0.92	0.84	0	0
Cumulative percentage variance:				
Of species data	9.20	12.80	22.30	29.70
Of species-environment relation	71.70	100.00	0	0
Total inertia	3.30			
Sum of all eigenvalues	2.04			
Sum of canonical eigenvalues	0.26			
Third measurement				
Eigenvalues	0.20	0.06	0.17	0.15
Species-environment correlations	0.94	0.86	0	0
Cumulative percentage variance:				
Of species data	9.90	13.10	21.50	29.20
Of species-environment relation	75.70	100.00	0	0
Total inertia	3.21			
Sum of all eigenvalues	1.99			
Sum of canonical eigenvalues	0.26			

Table 14: Correlations between environmental variables and canonical correspondence analysis axes at each measurement for 53 transects in short- and tall-tussock grassland communities. Elevation and solar radiation were used to constrain the axes. First measurement: 162 species, second measurement: 164 species, third measurement: 165 species.

	First measurement		Second measurement		Third measurement	
Correlations: CCA	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
Elevation	0.79	0.46	0.82	-0.39	0.86	-0.36
Solar radiation	0.44	0.80	-0.39	-0.76	-0.35	-0.80

Table 15: Results from tests of significance on canonical axes from canonical correspondence analysis for 53 transects in short- and tall-tussock grasslands. ** $P < 0.01$.

	F		
	First measurement	**Second measurement**	**Third measurement**
First canonical axis	3.84 **	3.96 **	4.29 **
All canonical axes	2.87 **	2.88 **	2.94 **

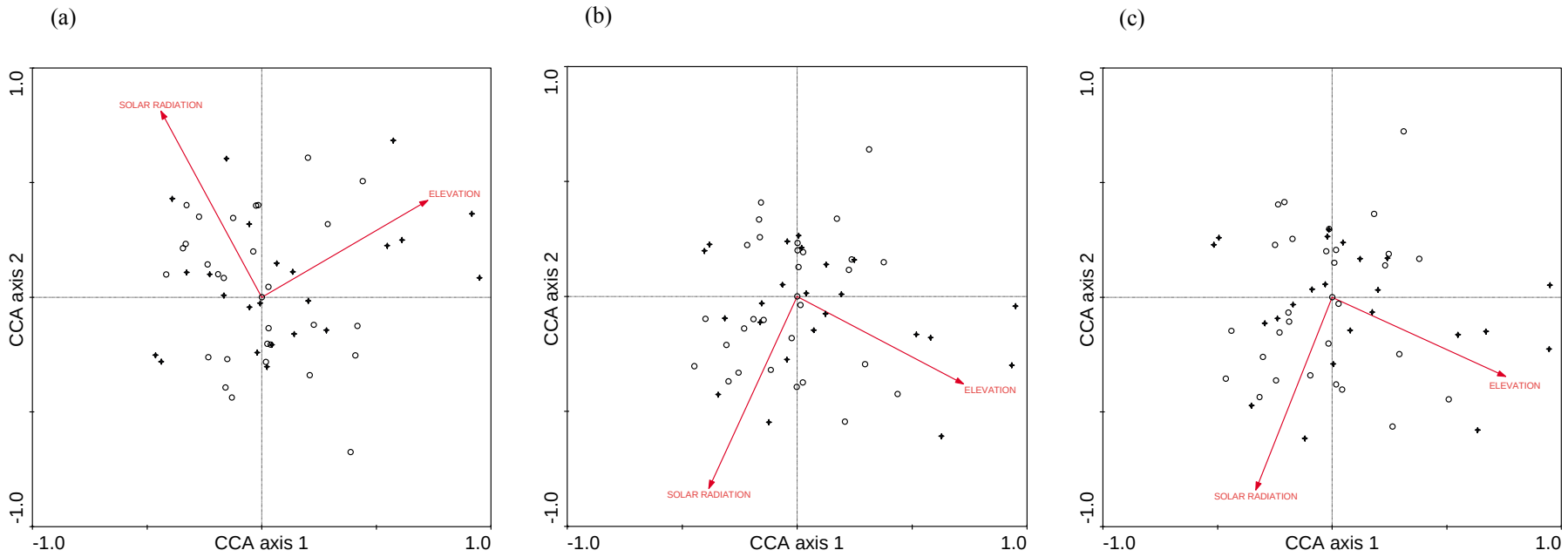

Figure 25: Scatterplots showing site scores and environmental variables from canonical correspondence analyses for 207 species on 53 transects in short- and tall-tussock grasslands for the first measurement (a), second measurement (b), and third measurement (c). Filled stars represent transects in conservation tenure, open circles represent transects in pastoral tenure. Arrows represent continuous environmental variables.

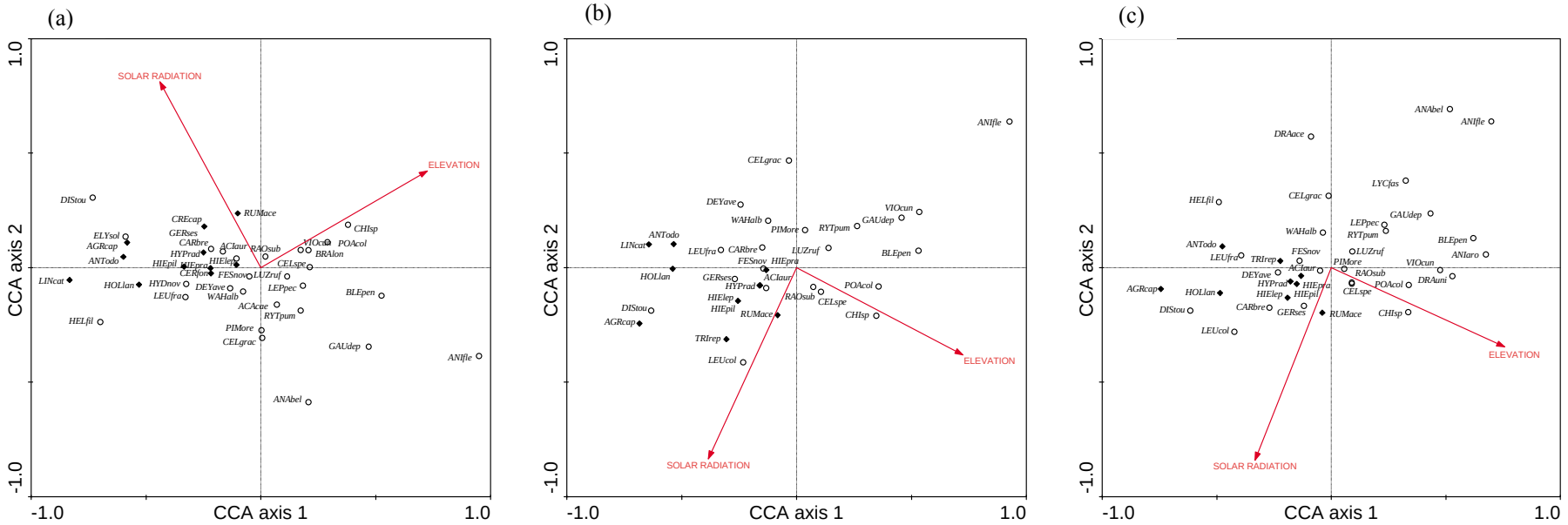

Figure 26: Scatterplots showing species scores and environmental variables from canonical correspondence analyses for 207 species on 53 transects in short- and tall-tussock grasslands for the first measurement (a), second measurement (b), and third measurement (c). Filled diamonds represent exotic species, open circles represent native species. Species shown have weights greater than 5%. For definitions of species codes see Appendix I.

4.3. Temporal patterns in species composition: short- and tall-tussock grassland communities (n=53)

Results from the CCAs for each measurement were very similar, indicating that there were no substantial changes in species composition between measurements. The distance that a transect moved between each measurement on the DCA scatterplot of transect scores is the equivalent of the amount that it changed in composition (Figure 27). Overall, transects changed more in species composition during the second time interval, compared with the first time interval (two-sample t-test: $t = 4.49$, d.f. = 92, $P < 0.001$, unequal variances). During the first time interval, transects that had higher solar radiation changed in composition more (Table 16, Figure 28). During the second time interval, the amount that transects changed in composition differed depending on which property they were on (Table 16). A Tukey test for multiple comparisons (Zar 1999) showed that transects on property 10 changed significantly less than those on properties 01 and 02 between the second and third measurements (Figure 28).

The direction that transects moved in ordination space between measurements is analogous to the nature of compositional change. For example, if a transect moved positively on the first axis, and positively on the second axis, native species are more abundant and characteristic of conservation tenure (Figure 24). During the first time interval the direction that transects changed in composition was significantly related to TWINSPAN community (Table 17). Transects in the tall-tussock grassland community were more likely to move towards having more native species (positively along the first axis, positively along on the second axis). In contrast, transects in the more modified short-tussock grassland community were more likely to move towards composition that was typical of disturbed areas (negatively on the first axis, and negatively on the second axis), which contained species such as *Anthoxanthum odoratum* and *Discaria toumatou* (Table 17).

During the second time interval, the direction that a transect moved in ordination space was significantly related to the property that it was on (Table 17). For example, all three transects on property 02 moved negatively on the first DCA axis and positively on the second DCA axis. Three of the four transects on property 06 moved negatively on the first DCA axis and negatively on the second DCA axis, towards more exotic species composition (Figure 24). Tenure was not significantly related to the direction that transects moved during the first time interval, or during the second time interval (Table 17).

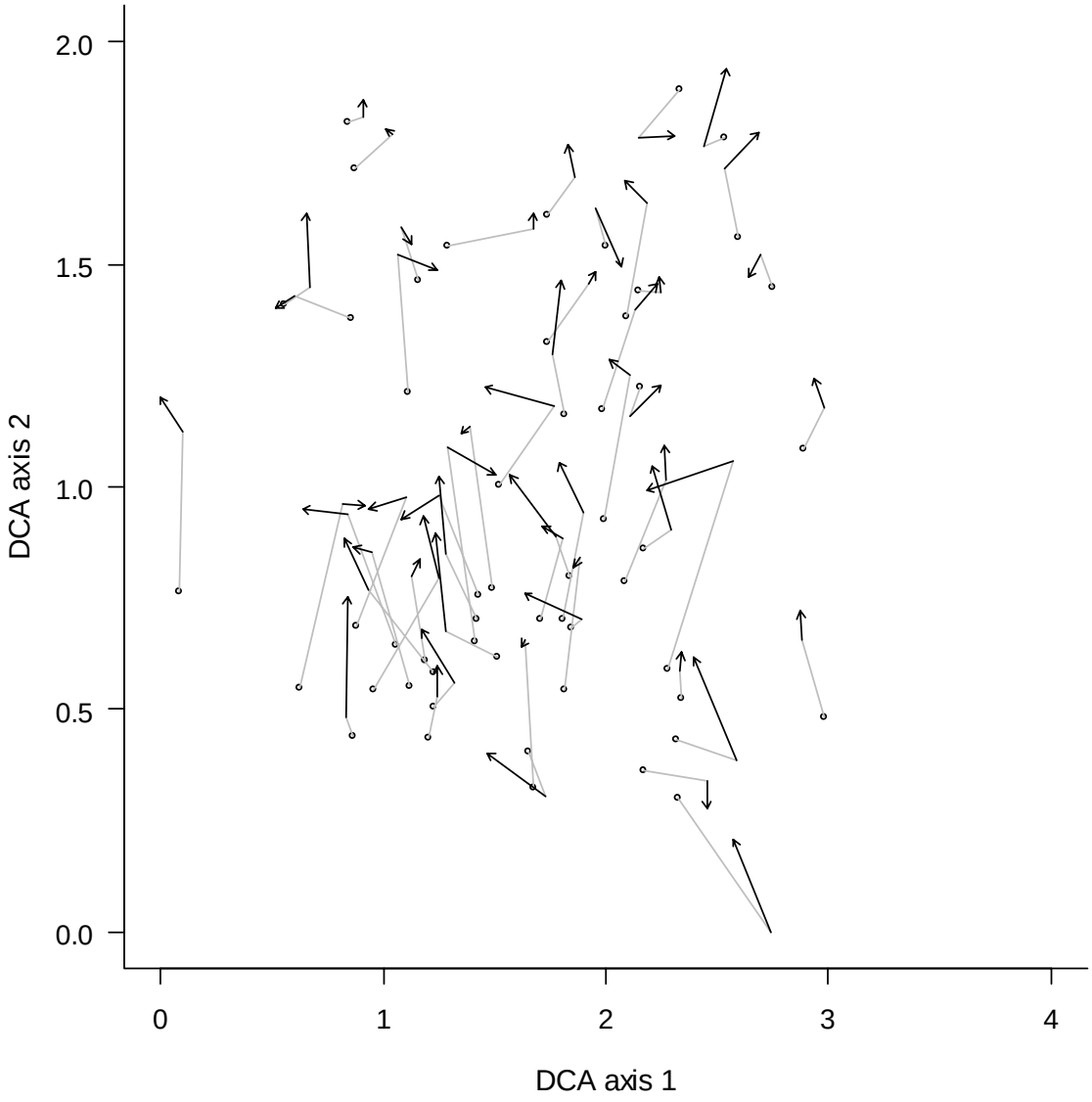

Figure 27: Scatterplot showing site scores from a detrended correspondence analysis of 207 species that occurred on 53 transects at three measurements in only the short- and tall-tussock grassland communities throughout Canterbury and Otago, showing changes in composition between each of the three measurements. Grey lines represent change in composition on one transect during the first time interval, black lines represent changes in composition during the second time interval.

Table 16: Results of analysis of variance tests and regression on the Euclidean distance between points over time on the first and second detrended correspondence analysis axes for 207 species that occurred on 53 transects in short- and tall-tussock grassland communities (i.e. amount of compositional change). * *P* < 0.05, ** *P* < 0.01, ns = not significant.

	Levels	*F* statistic of distance	
ANOVA: factor		**First time interval**	**Second time interval**
Property	12	2.01 ns	2.95 **
Tenure category	2	0.68 ns	0.67 ns
TWINSPAN community	2	1.30 ns	0.16 ns
Rock type	2	0.58 ns	2.99 ns
Soil type	2	3.76 ns	0.33 ns
Burnt	2	2.67 ns	1.29 ns
Regression: variable			
Elevation		1.36 ns	0.01 ns
Solar radiation		7.35 **	0.001 ns

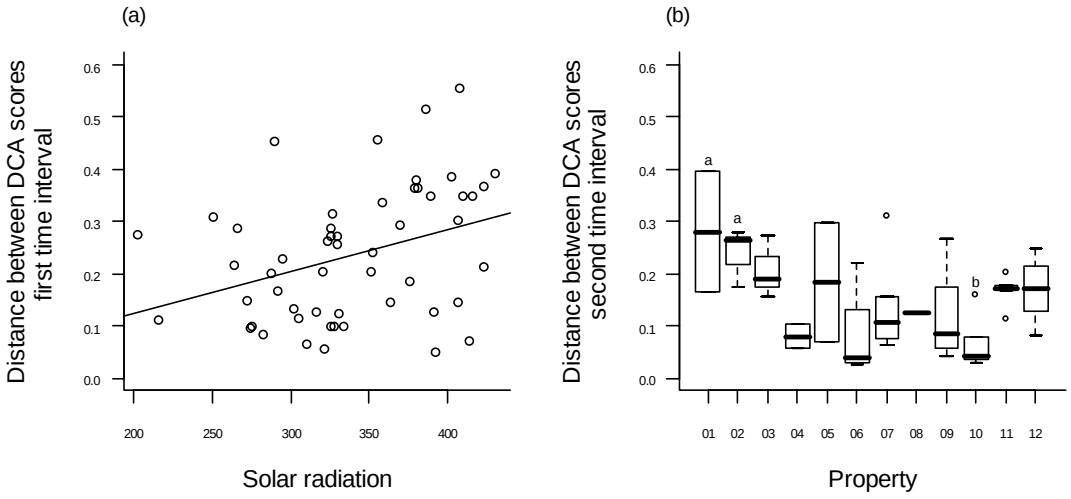

Figure 28: Variables that were significantly related to Euclidean distance between detrended correspondence analysis scores for 53 transects on short- and tall-tussock grasslands during the first time interval were solar radiation (a) and during the second time interval, property (b). The median distance for each property is the dark line, the upper and lower quartiles are represented by the outer ranges of the boxes, the upper and lower extremes are represented by the horizontal lines. The points represent outlying values for each property. Significant differences in distances are shown by a and b.

Table 17: Results of chi-square tests of independence and generalised linear models (Poisson link) for the direction of transect movement over time on the first and second detrended correspondence analysis axes for 207 species that occurred on 53 transects in short- and tall-tussock grassland communities (i.e. nature of compositional change). * $P < 0.05$, ** $P < 0.01$, ns = not significant.

	Levels	X^2 statistic for direction	
Chi-square tests: factor		**First time interval**	**Second time interval**
Property	12	39.93 ns	49.94 *
Tenure category	2	5.05 ns	6.46 ns
TWINSPAN community	2	13.00 **	3.57 ns
Rock type	2	2.71 ns	2.75 ns
Soil type	2	3.88 ns	5.23 ns
Burnt	2	5.25 ns	4.51 ns
Generalised linear models: variable		***Z*** **statistic of distance**	
Elevation		1.23 ns	-0.32 ns
Solar radiation		-0.61 ns	-1.10 ns

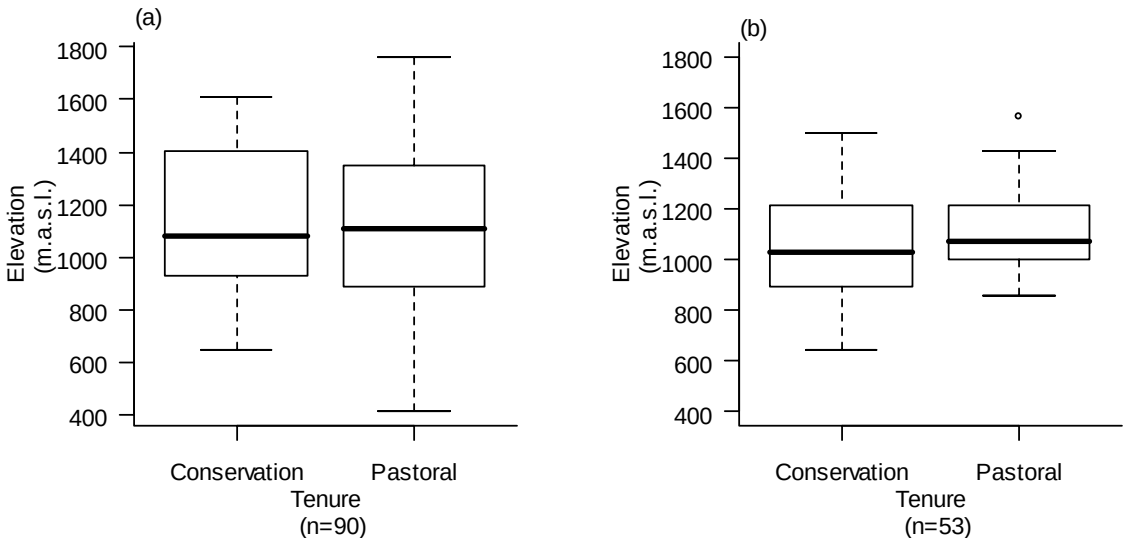

Figure 29: Boxplots showing relationship between tenure and elevation for 90 transects in tussock grasslands throughout Canterbury and Otago (a), and 53 transects in short- and tall-tussock grasslands (b). The median elevation for each tenure category is the dark line, the upper and lower quartiles are represented by the outer ranges of the boxes, the upper and lower extremes are represented by the horizontal lines. The points represent outlying values for each tenure category.

5. Discussion

The large amount of variation in species composition that is encompassed by these 90 transects was well-characterised by the division of transects into four community groups (Figure 18). The DCAs and the CCAs showed that there are important gradients in species composition and that these can be related to two of the measured environmental variables, elevation and solar radiation. Correlations between species composition and the measured environmental variables were not particularly strong, which is not surprising given the large size and high variability in the data set. These long and complex environmental gradients could account for the inconsistent temporal changes that occurred in these tussock grasslands. In other studies, tenure has been related to elevation, with transects at higher elevations being more likely to be in conservation tenure than pastoral tenure (Walker et al. 2006). However, there was no relationship between tenure and elevation in the present study for the 90 transects, or the 53 transects that were in short- and tall-tussock grassland communities (Figure 29).

I used TWINSPAN to define four community groups. Other studies in tussock grasslands that have used TWINSPAN have defined more community groups. For example, 15 communities were identified in the Kawarau Gorge, many of which were dominated by woody species such as *Rosa rubiginosa* and *Discaria toumatou* (Partridge et al. 1991). TWINSPAN in another highly modified area, Flat Top Hill, identified 14 community types (Walker et al. 1995). These studies were geographically restricted and contained much shorter gradients in species composition than the current study. The four broad TWINSPAN communities defined in the present study were ideal for demonstrating the long compositional gradient that was encompassed by these 90 transects across this large geographic area.

5.1. Environmental gradients in species composition

The variation in species composition is primarily a reflection of the large environmental variation that is encompassed by these transects, particularly in elevation. Species composition also reflected an elevational gradient in other studies in grasslands in Fiordland between 900 and 1600 m (Rose et al. 1988), in Central Otago below 460 m (Wilson et al. 1989) and in the Harper-Avoca Valley between 700 and 1350 m (Rose et al. 1995). Elevation is strongly correlated with species composition in tussock grasslands because several environmental variables, including temperature and precipitation, change with elevation. As

elevation increases, the climate in Central Otago becomes wetter and colder (Duncan 1965). Both temperature and soil moisture are important for determining patterns in species composition in tussock grasslands (Hubbard and Wilson 1988, Partridge et al. 1991, Walker and Lee 2000). At low elevations, the combination of low precipitation and high evaporation from intense solar radiation during summer, combined with intensive modification, has led to extensive areas of dry, "semi-desert" vegetation (Zotov 1938, Mark 1965d, Maunder 1965, Hubbard and Wilson 1988). These areas were classified as the highly-modified communities in the present study. Thus, the strong patterns in species composition with changing elevation may be related to differences in climate.

The elevation gradient also represented a gradient in soil chemistry. In particular, soil magnesium, calcium and pH were all negatively correlated with elevation (Table 6). These are important determinants of species distributions and composition in tussock grasslands (Archer 1973, Rose et al. 1988, Allen et al. 1997). High magnesium and calcium represent high soil fertility, which was related to species composition on the Ben Ohau Range, in the Upper Clutha and in the Mackenzie Basin (Archer 1973, Rose et al. 1988, Wilson et al. 1989, Norton et al. 2006). These changes in soil chemistry and fertility with elevation further explain why elevation was strongly related to species composition in the present study. In particular, exotic species are better adapted to high soil pH and high soil fertility, so can outcompete native species in these conditions (Wardle 1985, Scott et al. 1990, Allen et al. 1997, McIntosh et al. 1999, Scott et al. 2001, King and Wilson 2006, Norton et al. 2006). In the present study, soil fertility and pH were highest at low elevations, resulting in the dominance of exotic species at low elevations.

In tussock grasslands, the decreasing soil fertility and acidity gradients with increasing elevation may be reflecting a decreasing pastoral management gradient, because New Zealand's soils are naturally infertile (Wardle 1985, McLaren and Cameron 1996). Management is typically more intensive at low elevations (Molloy 1998, Walker and Lee 2002, Norton et al. 2006), which were historically the first areas to be cleared and grazed because they were easily accessible (Zotov 1938, Gibson and Bosch 1996, Vandvik and Birks 2002, Walker and Lee 2002). These areas continue to have high management inputs in that they are oversown and have fertiliser applied (Walker and Lee 2002). The ability of plants to respond to fertiliser depends on the climate, and therefore elevation. For example, nutrient inputs in high rainfall areas at high elevations can leach before plant uptake (McLaren and

Cameron 1996). Fertiliser addition can lower soil pH, which is often counteracted by liming, using calcium-based compounds (McLaren and Cameron 1996). High stock densities or sheep camps lead to soil compaction, resulting in losses of soil phosphorus, potassium and sulphur (McLaren and Cameron 1996). Both the soil fertility and acidity gradients are confounded with management differences at different elevations.

The abundance of exotic species at low elevations is consistent throughout New Zealand's South Island tussock grasslands, which demonstrates the importance of management in determining species composition (Wilson et al. 1989, Lloyd et al. 2003). More intensive management at low elevations may promote the establishment and growth of pastorally-productive exotic species (Walker and Lee 2002, Norton et al. 2006). Some exotic species can survive at higher elevations, indicating that they may have been dispersal-limited in the past, rather than having a habitat specialisation that limited them to lower elevations (Wilson 1989). Therefore, there may be a time lag before invasion occurs in tussock grasslands. This idea is supported by 37 years of monitoring in tussock grasslands in Marlborough, where exotic species were not abundant between 1959 and 1972, but had increased significantly by 1996 (Rose et al. 2004).

Solar radiation and elevation were important for species composition, and were almost orthogonal (Figure 25). Species composition changed more in areas with high solar radiation (Figure 28). Similar to elevation, changes in solar radiation reflect changes in other environmental variables because it was calculated from slope, aspect, and latitude. It is unclear how these variables relate to changes in composition.

Others have shown that *Hieracium* abundance declines at both extremely low and high elevations (Treskonova 1991, Duncan et al. 1997). This was also seen here, where *Hieracium* spp. were most abundant at mid-elevations (Figure 26). The initial patchy distribution of *Hieracium* spp. in tussock grasslands (Connor 1992b) indicates that they were initially dispersal-limited, but have now become widespread and can survive in a large range of conditions in tussock grasslands (Rose and Frampton 1999, Rose et al. 2004).

The exotic grasses, *Agrostis capillaris* and *Anthoxanthum odoratum,* increase in tussock grasslands after grazing cessation because they are successful at colonising gaps and disturbed

sites (Rose et al. 1995, Grove et al. 2002, Rose et al. 2004, Espie and Barratt 2006). *Anthoxanthum odoratum* can be outcompeted by other exotic species over time (Rose et al. 1995). There is some evidence for this occurring in the present study, where *Agrostis capillaris* and *Anthoxanthum odoratum* became less associated with each other over time (Figure 26). Calder et al. (1992) predicted that *Agrostis capillaris*-dominated communities will be replaced by native species, eventually leading to *Leptospermum*-dominated scrub. Further monitoring will be required in order to ascertain which of these outcomes may occur in these tussock grasslands in the long term.

Burning between the first and second measurements was not related to plant species composition or compositional change, which supports the idea that changes in composition caused by burning are reversible and temporary (Dickinson et al. 1992, Yeates and Lee 1997). There are indirect effects of burning that may impact plant species composition over longer periods of time. For example, soil depth was correlated with plant species composition on Flat Top Hill (Walker et al. 1995), and soil depth has been shown to be related to burning (Yeates and Lee 1997).

5.2. The effects of land management and tenure

Changes in composition after grazing by domestic stock has been removed are often unpredictable, inconsistent and weak (Grove et al. 2002, Meurk et al. 2002, Mark and Dickinson 2003, Smith 2003). Tenure was used in this study as an indication of differences in grazing. There was no strong gradient in species composition in relation to tenure, and transects in conservation tenure did not change in composition differently from transects in pastoral tenure. This may be because the transects in conservation tenure were clustered in space and may not have been truly independent (Figure 14). These factors indicate that removing grazing alone does not necessarily enhance native biodiversity (Norton 1988, Meurk et al. 1989, Lord 1990, Roper-Lindsay 2000). Importantly, areas in conservation tenure are unburnt as well as ungrazed, which may actually be necessary to maintain some native tussock grasslands (Calder et al. 1992).

Most plants in tussock grasslands are perennial and often slow growing, which means that vegetation change is slow (Sewell 1952, Rose and Platt 1992). On these transects, grazing has only been removed for a short period of time (mean = 28 years). Mark and Dickinson (2003)

also found inconsistent effects after grazing had been removed for 30 years. Because these communities have been grazed for over a century, we may expect it to take some time for vegetation dynamics in conservation land to become consistently different to areas in pastoral land.

Alternatively, the tenure categories may not adequately represent differences in management. Some areas in pastoral tenure are not grazed, for example, at high elevations where it is difficult to muster sheep (lessees, personal communications, 2005-2007; names with-held for confidentiality). This makes these areas similar to conservation tenure, in that they are not grazed by domestic stock and are not actively managed, i.e. no fertiliser, burning or oversowing of pastoral species. In the present study, many of these areas were in the high alpine mat-forming species community. Vegetation in conservation tenure may continue to be browsed by introduced herbivores that are pests, such as rabbits and deer (Jensen et al. 1997, personal observation). Over time, browsing by rabbits can have similar impacts to grazing by sheep (Wills and Beggs 1986).

Management factors are important for determining changes in species composition in tussock grasslands (O'Connor 1982, Allen et al. 1995). The present study shows that while management in the broad sense (tenure) may not influence changes in species composition, management at a localised scale (property) may. Each land manager has preconceived ideas about the outcomes that they aim to achieve for the land that they administer. On properties in pastoral tenure, this will determine factors such as stocking rates, fertiliser application, burning frequency, and which species will be oversown. This directs compositional change towards that desired outcome (lessee, personal communications, 2005-2007; names with-held for confidentiality). Even properties within conservation tenure will be managed differently. For example, areas that have higher visitor numbers may have more weed management. These property-level differences in management may also explain why there were no overall directional trends in changes in species composition over time.

The idea that management is an important determinant of changes in species composition in these tussock grasslands is further supported by the fact that changes in composition differed according to community type. Short-tussock grasslands are generally more actively managed than tall-tussock grasslands, in that they are burned and oversown more frequently (Espie and Barratt 2006). Burning to create and maintain the short-tussock grassland communities may

make them more susceptible to invasion by exotic species (Meurk et al. 2002). Meurk et al. (2002) found that short-tussock grasslands were more prone to invasion by exotic species than tall-tussock grasslands in the Mackenzie Basin over 10 years, which was also found in the present study. These results indicate that management at the property level are important, and are not detected by the general tenure variable.

However, community type may have been significantly related to the direction of change in composition because the initial species composition of an area will influence the how composition will change (Egler 1954, Rose et al. 1995, Grove et al. 2002). This is because seed sources are limited to the species that are present in, or adjacent to the area. These interactions between initial species composition, elevation and management make it difficult to distinguish between human influences and ecological drivers of compositional change in these tussock grasslands. Furthermore, we cannot make any general landscape-level predictions about changes in composition that may occur in tussock grasslands over time.

6. Conclusions

Overall, these results show that there are distinct communities of vascular plant species on these 90 transects in tussock grasslands in Otago and Canterbury. Of the measured environmental variables, elevation and solar radiation were strongly related to species composition, which is probably because it represents changes in management, soil chemistry and climate. However, it is difficult to quantify the effects of environmental variables on species composition because they are often not independent of each other, and interact with management. Management appears to be important for changes in species composition in both space and time, which is represented by elevation and property-level differences in plant compositional change.

There have been no large, consistent shifts in species composition in these tussock grasslands over the past 24 years. Although changes in plant species composition were related to solar radiation, property and TWINSPAN community, these relationships were weak and were not consistent over time. The high variability in management and environmental variables makes it difficult to make any clear predictions about how composition will change in tussock grasslands in the future and highlights the importance of continued monitoring on these transects.

Chapter 4: General Discussion

The aim of this thesis was to investigate changes in vascular plant species richness and composition of tussock grasslands over the last 24 years, and to relate these changes to environmental variables and land tenure. The data are from 90 permanently-marked transects located throughout Canterbury and Otago that have been measured between 1982 and 1986, were remeasured between 1993 and 1999, and again between 2005 and 2006.

These data provide one of the most comprehensive, long-term records of vegetation change in New Zealand's South Island tussock grasslands, covering a wide range of environmental conditions and located over a wide geographic region throughout Canterbury and Otago. The transects were able to be accurately relocated because they were marked in the field, and consistency in species identifications was ensured by having the same botanist involved in species identifications at each measurement. Transects in this data set are also on land that is in both conservation and pastoral tenure, which is unusual considering that most ecological studies in New Zealand are on public conservation land (Norton 2001).

1. Key results

This thesis investigated changes in community structure in tussock grasslands based on eight objectives, which were outlined in the introduction. Over time, changes in community structure were inconsistent and unpredictable. Species richness declined on most transects between the first and second measurements, but increased on most transects between the second and third measurements. These changes occurred regardless of tenure category, and were best related to rock type and elevation. Elevation was also strongly related to spatial variation in species composition, because the TWINSPAN communities were well-separated along an elevation gradient. Spatial variation in composition was related primarily to elevation and solar radiation. The composition of transects did not change considerably over time. The amount and nature of compositional change over time was related to solar radiation, property and TWINSPAN community. This means that transects on some properties changed more in species composition than others, and transects on some properties were more likely to change in a particular way, for example, they were more likely to become dominated by native species. Tenure was not related to the species composition gradient, or temporal changes in species composition.

Species composition changed more between the first and second measurements, when species richness declined, compared to between the second and third measurements, when species richness increased. This means that those species that were present at the second measurement increased in abundance at the quadrat scale, but fewer new species colonised transects between the second and third measurements. This pattern was also observed in the changes in total transect species richness, where fewer species groups increased between the second and third measurements. These local extinctions and declines in species abundances could have occurred because many plants in tussock grasslands are dispersal limited (Spence 1990). Therefore, once certain species became locally rare or extinct, they did not re-colonise and increase in abundance. A similar explanation was given for the loss of sub-dominant herbs in the Black Rock Scientific Reserve over 30 years (Mark and Dickinson 2003).

In contrast with other studies, there was no evidence that exotic species were driving the overall changes in species richness and composition (Rose et al. 1995, Walker 2000, Meurk et al. 2002). This is because both native and exotic species declined in mean quadrat species richness between the first and second measurements, but only native species richness increased at the third measurement. This could be because exotic species were abundant only at low elevations.

However, the invasive exotic herb, *Hieracium* spp. (*H. lepidulum, H. pilosella, H. prealtum, H. caespitosa, H. auranticum*), increased over the 24 years of this study. This is consistent with other studies, where *Hieracium* has increased in many areas regardless of original species composition and management (Treskonova 1991, Connor 1992b, Rose et al. 2004).

2. Outcomes and implications

Elevation was strongly related to patterns in species composition and changes in species richness. Changes in elevation represent changes in other environmental variables, including precipitation, temperature and soil chemistry, which are important for determining vegetation patterns in tussock grasslands (Hubbard and Wilson 1988, Rose et al. 1995, Allen et al. 1997, Walker and Lee 2000, Mark and Dickinson 2003).

Increasing elevation also represents decreasing management intensity (Gibson and Bosch 1996, Walker and Lee 2000). The importance of management for determining community structure, in terms of fertilisers, burning and grazing, is well-documented in tussock grasslands (e.g., O'Connor 1981, Allen et al. 1995, Norton et al. 2006). The significant relationship between property and compositional change may reflect management differences by property. However, these effects were inconsistent, indicating that changes in community structure in tussock grasslands are likely to be caused by a combination of environmental, management and ecological factors. These factors are inherently linked so that the physical location of a lease will determine how it is managed.

The present study shows that management in the broad sense (tenure) has not influenced changes in species composition. However, management at the property-scale may be important. This could be because tenure may not accurately represent differences in grazing; areas within conservation tenure continue to be grazed by introduced pests, and within pastoral tenure there are areas that are no longer grazed. In saying this, transects in conservation tenure have only changed tenure recently, relative to the length of time that we would expect change to occur in tussock grasslands. It is possible that there will be more consistent changes within each tenure category as these areas continue to be ungrazed by domestic stock, highlighting the importance of remeasuring these transects in the future.

Overall, the changes in the community structure of these tussock grasslands are related to a combination of environmental factors, such as soil chemistry and climate, and management factors. The inconsistent changes that have occurred on these 90 transects over the past 24 years, and the nature and complexity of the variables that explain those changes, make it difficult to be able to make any clear predictions about future changes that may occur. However, this research shows that the conversion of pastoral lease land to conservation tenure has not, so far, had a large impact on changes in plant species composition or species richness in these tussock grasslands. This highlights the importance of continued monitoring of these permanent transects and other tussock grassland sites for many years into the future if we are to obtain a good understanding of the effects of land use on vegetation change.

3. Further research and recommendations:

These 90 transects contain detailed and accurate information about plant communities in South Island tussock grasslands. This study demonstrates the importance of remeasuring these transects at relatively short time intervals, in order to gain a deeper understanding of changes that are occurring in these human-induced landscapes. I recommend that these 90 transects continue to be re-measured at intervals of no longer 10 years (Hunter and Scott 1997). Future consistency in species identification is possible because specimens of most of the species are to be deporsited in the Lincoln University herbarium collection.

This study also showed that this method of 100 m transects, with 0.25 m^2 quadrats placed every two metres, is an effective method for detecting changes in both species richness and composition over time. Using a standardised method for all tussock grassland transects would allow comparison between areas and studies of tussock grasslands (Allen 1993).

Although difficult, it would be worthwhile collecting detailed, accurate information about management history and environmental variables for all long-term tussock grassland studies. This would enable a better understanding of the processes driving vegetation change. On these transects in particular, soil chemistry variables should be collected at each remeasurement, because these are also likely to fluctuate over time (McLaren and Cameron 1996).

Currently, we cannot make any broad generalisations about vegetation change in relation to tenure category. This may be possible once these areas have been in conservation tenure for a longer period of time, and when a larger range of community types have been encompassed into conservation tenure through the Tenure Review process.

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Appendix I: Species codes and full botanical names for the 347 species that were recorded over all three measurement times on all 90 transects. Each species was classified into one of two "origin" classes (native=N, exotic=I), one of two longevity classes (annual=A, perennial=P), and one of eight growth form classes (*Hieracium* spp.=HIE, *Chionochloa* spp.=CHIsp, woody species=S, grasses (excluding *Chionochloa*)=G, small herbs (<2 cm tall)=H1, large herbs (>2 cm tall)=H2, ferns=F, rushes/sedges=R). (nomenclature follows Anon 2006)

Species Code	Botanical Name	Origin	Longevity	Growth Form
ABRcae	*Abrotanella caespitosa*	N	P	H1
ABRinc	*Abrotanella inconspicua*	N	P	H1
ACAagn	*Acaena agnipila*	I	P	H2
ACAbuc	*Acaena buchananii*	N	P	H2
ACAcae	*Acaena caesiiglauca*	N	P	H2
ACAfis	*Acaena fissistipula*	N	P	H1
ACAine	*Acaena inermis*	N	P	H2
ACAnov	*Acaena novae-zelandiae*	N	P	H2
ACAsac	*Acaena saccaticupula*	N	P	H2
ACAtes	*Acaena tesca*	N	P	H1
ACHmil	*Achillea millefolium*	I	P	H2
ACIaur	*Aciphylla aurea*	N	P	H2
ACIcol	*Aciphylla colensoi*	N	P	H2
ACIhec	*Aciphylla hectori*	N	P	H2
ACIlom	*Aciphylla lomondii*	N	P	H2
ACImonr	*Aciphylla monroi*	N	P	H2
ACImont	*Aciphylla montana*	N	P	H2
ACIsim	*Aciphylla similis*	N	P	H2
AGRcap	*Agrostis capillaris*	I	P	G
AGRmue	*Agrostis muelleriana*	N	P	G
AGRmus	*Agrostis muscosa*	N	P	G
AGRpal	*Agrostis pallescens*	N	P	G
AGRper	*Agrostis personata*	N	P	G
AGRpet	*Agrostis petriei*	N	P	G
AIRcar	*Aira caryophyllea*	I	A	G
ANAarv	*Anagallis arvensis*	I	A	H1
ANAbel	*Anaphalioides bellidioides*	N	P	H1
ANIaro	*Anisotome aromatica*	N	P	H2
ANIfil	*Anisotome filifolia*	N	P	H2

ANIfle	*Anisotome flexuosa*	N	P	H2
Species Code	Botanical Name	Origin	Longevity	Growth Form
ANIimb	*Anisotome imbricata*	N	P	H1
ANIlan	*Anisotome lanuginosa*	N	P	H1
ANTodo	*Anthoxanthum odoratum*	I	P	G
APHarv	*Aphanes arvensis*	I	A	H1
AREser	*Arenaria serpyllifolia*	I	A	H1
ARRela	*Arrhenatherum elatius*	I	P	G
ASPflab	*Asplenium flabellifolium*	N	P	F
BLEpen	*Blechnum penna-marina*	N	P	F
BRAbel	*Brachyglottis bellidioides*	N	P	H2
BRAhaa	*Brachyglottis haastii*	N	P	H2
BRAlon	*Brachyscome longiscapa*	N	P	H1
BRArad	*Brachyscome radicata*	N	P	H1
BROdia	*Bromus diandrus*	I	A	G
BROhor	*Bromus hordeaceus*	I	A	G
BROtec	*Bromus tectorum*	I	A	G
BULang	*Bulbinella angustifolia*	N	P	H2
CARalp	*Carpha alpina*	N	P	R
CARbil	*Cardamine bilobata*	N	P	H2
CARbre	*Carex breviculmis*	N	P	R
CARcol	*Carex colensoi*	N	P	R
CARcur	*Carmichaelia curta*	N	P	S
CARdcor	*Cardamine corymbosa*	N	P	H2
CARech	*Carex echinata*	N	P	R
CAREkir	*Carex kirkii var kirkii*	N	P	R
CARgau	*Carex gaudichaudiana*	N	P	R
CARhec	*Carex hectori*	N	P	R
CARMkir	*Carmichaelea kirkii*	N	P	S
CARmon	*Carmichaelia monroi*	N	P	S
CARMpet	*Carmichaelia petriei*	N	P	S
CARnut	*Carduus nutans*	I	A	H2
CARpyr	*Carex pyrenaica*	I	P	H2
CARten	*Carduus tenuiflorus*	I	A	H2
CARvex	*Carmichaelia vexillata*	N	P	S
CARwak	*Carex wakatipu*	N	P	R
CASful	*Cassinia fulvida*	N	P	S
CASvau	*Cassinia vauvilliersii*	N	P	S
CELalp	*Celmisia alpina*	N	P	H2
CELang	*Celmisia angustifolia*	N	P	H2
CELden	*Celmisia densiflora*	N	P	H2
CELdur	*Celmisia du-rietzii*	N	P	H2

CELgla	*Celmisia glandulosa*	N	P	H1
Species Code	Botanical Name	Origin	Longevity	Growth Form
CELgrac	*Celmisia gracilenta*	N	P	H2
CELhaa	*Celmisia haastii*	N	P	H2
CELlar	*Celmisia laricifolia*	N	P	H1
CELlya	*Celmisia lyallii*	N	P	H2
CELses	*Celmisia sessiliflora*	N	P	H1
CELspe	*Celmisia spectabilis*	N	P	H2
CELves	*Celmisia vespertina*	N	P	H2
CELvis	*Celmisia viscosa*	N	P	H2
CENery	*Centaurium erythraea*	N	A	H2
CERfon	*Cerastium fontanum*	I	P	H2
CERglo	*Cerastium glomeratum*	I	A	H2
CHEfas	*Cheesemania fastigiata*	N	P	H2
CHEsie	*Cheilanthes humilis*	N	P	F
CHIden	*Chionohebe densifolia*	N	P	H1
CHIpul	*Chionohebe pulvinaris*	N	P	H1
CHIsp	*Chionochloa sp*	N	P	CHIsp
CHItho	*Chionohebe thomsonii*	N	P	H1
CIRarv	*Cirsium arvense*	I	P	H2
CIRvul	*Cirsium vulgare*	I	A	H2
COLape	*Colobanthus apetalus*	N	P	H1
COLbre	*Colobanthus brevisepalus*	N	P	H1
COLstr	*Colobanthus strictus*	N	P	H1
CONver	*Convolvulus verecundus*	N	P	H2
COPatr	*Coprosma atropurpurea*	N	P	S
COPche	*Coprosma cheesmanii*	N	P	S
COPper	*Coprosma perpusilla*	N	P	S
COPpet	*Coprosma petriei*	N	P	S
CORcra	*Corallospartium crassicaule*	N	P	S
CORplu	*Coriaria plumosa*	N	P	H2
CRAinc	*Craspedia incana*	N	P	H2
CRAlan	*Craspedia lanata*	N	P	H2
CRAsie	*Crassula sieberiana*	N	P	H2
CRAtet	*Crassula tetramera*	N	A	H2
CRAunif	*Craspedia uniflora*	N	P	H2
CREcap	*Crepis capillaris*	I	A	H2
CYNcri	*Cynosurus cristatus*	I	P	G
DACglo	*Dactylis glomerata*	I	P	G
DEScha	*Deschampsia chapmanii*	N	P	R
DESnov	*Deschampsia novae-zelandiae*	N	P	G
DEYave	*Deyeuxia avenoides*	N	A	G

DIAarm	*Dianthus armeria*	I	A	H2
Species Code	Botanical Name	Origin	Longevity	Growth Form
DICcri	*Dichelachne crinita*	N	A	G
DICrep	*Dichondra repens*	N	P	H1
DIStou	*Discaria toumatou*	N	P	S
DOLsco	*Dolichoglottis scorzoneroides*	N	P	H2
DRAace	*Dracophyllum acerosum*	N	P	S
DRAlon	*Dracophyllum longifolium*	N	P	S
DRAmus	*Dracophyllum muscoides*	N	P	S
DRApol	*Dracophyllum politum*	N	P	S
DRApron	*Dracophyllum pronum*	N	P	S
DRAuni	*Dracophyllum uniflorum*	N	P	S
DROarc	*Drosera arcturi*	N	P	H1
ECHvul	*Echium vulgare*	I	A	H2
ELYrec	*Elymus rectisetus*	N	A	G
ELYsol	*Elymus solandri*	N	A	G
EPIals	*Epilobium alsinoides*	N	A	H1
EPIatr	*Epilobium atriplicifolium*	N	A	H1
EPIhec	*Epilobium hectori*	N	A	H1
EPIkom	*Epilobium komarovianum*	N	A	H1
EPIpyc	*Epilobium pycnostochyum*	N	A	H1
EROcic	*Erodium cicutarium*	I	A	H1
EROver	*Erophila verna*	I	A	H1
EUCrua	*Euchiton ruahinicum*	N	P	H2
EUPdye	*Euphrasia dyeri*	N	P	H1
EUPzel	*Euphrasia zelandica*	N	P	H1
FESmad	*Festuca madida*	N	P	G
FESmat	*Festuca matthewsii*	N	P	G
FESmul	*Festuca multinodis*	N	P	G
FESnov	*Festuca novae-zelandiae*	N	P	G
FESrub	*Festuca rubra*	N	P	G
FESten	*Festuca tenuifolia*	I	P	G
FORsed	*Forstera sedifolia*	N	P	H2
GAIset	*Gaimardia setacea*	N	P	R
GALper	*Galium perpusillum*	N	P	H2
GAUcra	*Gaultheria crassa*	N	P	S
GAUdep	*Gaultheria depressa var. nov.*	N	P	S
GAUnub	*Gaultheria nubicola*	N	P	S
GENama	*Gentiana amabilis*	N	P	H2
GENbell	*Gentiana bellidifolia*	N	P	H2
GENcor	*Gentiana corymbifera*	N	P	H2
GENdiv	*Gentiana divisa*	N	P	H2

GERmic	*Geranium microphyllum*	N	P	H1
Species Code	Botanical Name	Origin	Longevity	Growth Form
GERses	*Geranium sessiliflorum*	N	P	H1
GEUlei	*Geum leiospermum*	N	P	H1
GEUpar	*Geum parviflorum*	N	P	H2
GINdec	*Gingidia decipiens*	N	P	H2
GNAaux	*Gnaphalium audax*	N	P	H2
GNAlat	*Gnaphalium laterale*	N	P	H1
GNAlut	*Gnaphalium luteo-album*	N	P	H2
GNAmac	*Gnaphalium mackayi*	N	P	H1
GONagg	*Gonocarpus aggregatus*	N	P	H2
GONmic	*Gonocarpus micranthus*	N	P	H2
GONmon	*Gonocarpus montanus*	N	P	H2
GRAgiv	*Grammitis givenii*	N	P	F
HEBbuc	*Hebe buchananii*	N	P	S
HEBhaa	*Hebe haastii*	N	P	S
HEBlyc	*Hebe lycopodioides*	N	P	S
HEBtet	*Hebe tetrasticha*	N	P	S
HECcae	*Hectorella caespitosa*	N	P	H1
HELfil	*Helichrysum filicaule*	N	P	H2
HELplu	*Helichrysum plumeum*	N	P	S
HIEaur	*Hieracium aurantiacum*	I	P	HIE
HIEcae	*Hieracium caespitosum*	I	P	HIE
HIEequ	*Hierochloe equiseta*	N	P	G
HIElep	*Hieracium lepidulum*	I	P	HIE
HIEnov	*Hierochloe novae-zelandiae*	N	P	G
HIEpil	*Hieracium pilosella*	I	P	HIE
HIEpra	*Hieracium praeltum*	I	P	HIE
HIErec	*Hierochloe recurvata*	N	P	G
HOLlan	*Holcus lanatus*	I	P	G
HYDmon	*Hydrocotyle montana*	N	P	H1
HYDnov	*Hydrocotyle novae-zelandiae*	N	P	H1
HYPgra	*Hypericum gramineum*	I	A	H2
HYPmil	*Hypolepis millefolium*	N	P	F
HYPper	*Hypericum perforatum*	I	A	H2
HYPrad	*Hypochoeris radicata*	I	P	H1
ISOauk	*Isolepis aucklandica*	N	P	R
JUNant	*Juncus antarticus*	N	P	R
KELchi	*Kelleria childii*	N	P	H1
KELdie	*Kelleria dieffenbachii*	N	P	H1
KELpad	*Kelleria padulosa*	N	P	H1
KELvil	*Kelleria villosa*	N	P	H1

KOEnov	*Koeleria novae-zelandiae*	N	P	G
Species Code	Botanical Name	Origin	Longevity	Growth Form
KOEshe	*Koeleria cheesemanii*	N	A	G
KRInov	*Kirkianella novae-zelandiae*	N	P	H1
KUNeri	*Kunzea ericoides*	N	P	S
LACfil	*Lachnagrostis filiformis*	N	A	G
LAClya	*Lachnagrostis lyallii*	N	P	G
LAGcun	*Lagenifera cuneata*	N	P	H1
LAGpet	*Lagenifera petiolata*	N	P	H1
LEPatr	*Leptinella atrata*	N	P	H1
LEPgoy	*Leptinella goyenii*	N	P	H1
LEPpec	*Leptinella pectinata*	N	P	H1
LEPpus	*Leptinella pusilla*	N	P	H1
LEPsco	*Leptospermum scoparium*	N	P	S
LEPser	*Leptinella serrulata*	N	P	H1
LEPsqu	*Leptinella squalida*	N	P	H1
LEUcol	*Leucopogon colensoi*	N	P	S
LEUfra	*Leucopogon fraseri*	N	P	S
LEUgra	*Leucogenes grandiceps*	N	P	H2
LINcat	*Linum catharticum*	I	A	H2
LOBlin	*Lobelia linnaeoides*	N	P	H1
LOLper	*Lolium perenne*	I	P	G
LOTped	*Lotus pedunculatus*	I	P	H2
LUZlep	*Luzula leptophylla*	N	P	R
LUZpum	*Luzula pumila*	N	P	R
LUZruf	*Luzula rufa*	N	P	R
LUZulo	*Luzula ulophylla*	N	P	R
LYCfas	*Lycopodium fastigiatum*	N	P	H2
MARvul	*Marrubium vulgare*	I	P	H2
MELalp	*Melicytus alpinus*	N	P	S
MENcun	*Mentha cunninghamii*	N	P	H2
MICsca	*Microseris scapigera*	N	P	H2
MICuni	*Microtis unifolia*	N	P	H2
MONfon	*Montia fontana*	N	P	H1
MRYnum	*Myrsine nummularia*	N	P	S
MUEaxi	*Muehlenbeckia axillaris*	N	P	S
MUEcom	*Muehlenbeckia complexa*	N	P	S
MYOdis	*Myosotis discolor*	I	A	H2
MYOdru	*Myosotis pygmaea var. drucei*	N	P	H1
MYOpul	*Myosotis pulvinaris*	N	P	H1
MYOpyg	*Myosotis pygmaea*	N	P	H1
MYOstr	*Myosotis stricta*	I	A	H1

NAVsqu	*Navarettia squarrosa*	I	A	H2
Species Code	Botanical Name	Origin	Longevity	Growth Form
NEOaus	*Neopaxia australasica*	N	P	H1
NERbal	*Nertera balfouriana*	N	P	H1
NERset	*Nertera setulosa*	N	P	H1
OLEodo	*Olearia odorata*	N	P	S
OPHcor	*Ophioglossum coriaceum*	N	P	H1
OREcol	*Oreomyrrhis colensoi*	N	P	H2
OREpec	*Oreobolus pectinatus*	N	P	R
OREram	*Oreomyrrhis ramosa*	N	P	H2
ORErig	*Oreomyrrhis rigida*	N	P	H2
OREsub	*Oreostylidium subulatum*	N	P	H1
OROmin	*Orobanche minor*	I	P	H2
OURcae	*Ourisia caespitosa*	N	P	H1
OURgla	*Ourisia glandulosa*	N	P	H1
OURsim	*Ourisia simpsonii*	N	P	H2
OXAexi	*Oxalis exilis*	N	P	H1
PENpum	*Pentachondra pumila*	N	P	H1
PHOcoo	*Phormium cookianum*	N	P	H2
PHYcol	*Phyllachne colensoi*	N	P	H1
PHYrub	*Phyllacne rubra*	N	P	H1
PIMore	*Pimelea oreophila*	N	P	S
PIMpse	*Pimelea pseudo-lyallii*	N	P	S
PIMtra	*Pimelea traversii*	N	P	S
PLAlani	*Plantago lanigera*	N	P	H1
PLAuni	*Plantago uniflora*	N	P	H1
POAann	*Poa annua*	I	P	G
POAbre	*Poa breviglumis*	N	P	G
POAcit	*Poa cita*	N	P	G
POAcol	*Poa colensoi*	N	P	G
POAint	*Poa intrusa*	N	P	G
POAkir	*Poa kirkii*	N	P	G
POAlin	*Poa lindsayi*	N	A	G
POAman	*Poa maniototo*	N	P	G
POApra	*Poa pratensis*	I	P	G
POAton	*Poa tonsa*	N	P	G
PODniv	*Podocarpus nivalis*	N	P	S
POLves	*Polystichum vestitum*	N	P	F
PRAang	*Pratia angulata*	N	P	H1
PRAcol	*Prasophyllum colensoi*	N	P	H2
PRAmac	*Pratia macrodon*	N	P	H1
PRUvul	*Prunella vulgaris*	I	P	H2

PSYnov	*Psychrophila novae-zelandiae*	N	P	H1
Species Code	Botanical Name	Origin	Longevity	Growth Form
PSYobt	*Psychrophila obtusa*	N	P	H1
PTEcyc	*Pterostylis cycnocephala*	N	P	H1
PTEesc	*Pteridium esculentum*	N	P	F
PTEmut	*Pterostylis mutica*	N	P	H1
PTEven	*Pterostylis venosa*	N	P	H2
RANeny	*Ranunculus enysii*	N	P	H1
RANfol	*Ranunculus foliosus*	N	P	H1
RANgra	*Ranunculus gracilipes*	N	P	H1
RANmul	*Ranunculus multiscapus*	N	P	H1
RANroy	*Ranunculus royi*	N	P	H1
RAOaus	*Raoulia australis*	N	P	H1
RAObea	*Raoulia beauverdii*	N	P	H1
RAOexi	*Raoulia eximia*	N	P	H1
RAOgra	*Raoulia grandiflora*	N	P	H1
RAOhec	*Raoulia hectorii*	N	P	H1
RAOhoo	*Raoulia hookeri*	N	P	H1
RAOpar	*Raoulia parkii*	N	P	H1
RAOsub	*Raoulia subsericea*	N	P	H1
RAOten	*Raoulia tenuicaulis*	N	P	H1
ROSgra	*Rostkovia magellanica*	N	P	R
ROSrub	*Rosa rubiginosa*	I	P	S
RUMace	*Rumex acetosella*	I	P	H1
RUMobt	*Rumex obtusifolius*	I	P	H2
RYTaus	*Rytidosperma australe*	N	P	G
RYTmac	*Rytidosperma maculatum*	N	P	G
RYTpum	*Rytidosperma pumilum*	N	P	G
RYTset	*Rytidosperma setifolium*	N	P	G
RYTtho	*Rytidosperma thomsonii*	N	P	G
SCHcoc	*Schizeilema cockaynei*	N	P	H1
SCHcya	*Schizeilema haastii var cyanopeta*	N	P	H2
SCHexi	*Schizeilema exiguum*	N	P	H1
SCHhyd	*Schizeilema hydrocotyloides*	N	P	H1
SCHpau	*Schoenus pauciflorus*	N	P	R
SCLbro	*Scleranthus brockiei*	N	P	H1
SCLuni	*Scleranthus uniflorus*	N	P	H1
SEDacr	*Sedum acre*	I	P	H1
SENqua	*Senecio quadridentatus*	N	P	H2
SILcon	*Silene conica*	I	A	H2
SILgal	*Silene gallica*	I	A	H2

SPErub	*Spergularia rubra*	I	A	H1
Species Code	Botanical Name	Origin	Longevity	Growth Form
STAmin	*Stackhousia minima*	N	P	H1
STEgrac	*Stellaria gracilenta*	N	P	H1
TARmag	*Taraxacum magellanicum*	N	P	H2
TARoff	*Taraxacum officinale*	I	P	H2
THElon	*Thelymitra longifolia*	N	P	H2
THYvul	*Thymus vulgaris*	I	P	S
TRIarv	*Trifolium arvense*	I	A	H2
TRIdub	*Trifolium dubium*	I	A	H1
TRIglo	*Trifolium glomeratum*	I	A	H2
TRIhyb	*Trifolium hybridum*	I	P	H2
TRIpra	*Trifolium pratense*	I	P	H2
TRIrep	*Trifolium repens*	I	P	H2
TRIspi	*Trisetum spicatum*	N	P	G
UNCdiv	*Uncinia divaricata*	N	P	R
UNCfus	*Uncinia fuscovaginata*	N	P	R
UNCsin	*Uncinia sinclairii*	N	P	R
UNCvir	*Uncinia viridis*	N	P	R
URTure	*Urtica urens*	N	A	H2
UTRmon	*Utricularia monanthos*	N	A	H1
VERarv	*Veronica arvensis*	I	A	H2
VERser	*Veronica serpyllifolia*	I	A	H2
VERtha	*Verbascum thapsus*	I	A	H2
VERvir	*Verbascum virgatum*	I	A	H2
VICsat	*Vicia sativa*	I	P	H2
VIOcun	*Viola cunninghamii*	N	P	H2
VITaus	*Vittadinia australis*	N	P	H2
VULbro	*Vulpia bromoides*	I	A	G
WAHalb	*Wahlenbergia albomarginata*	N	P	H1
WAHgra	*Wahlenbergia gracilis*	N	P	H1

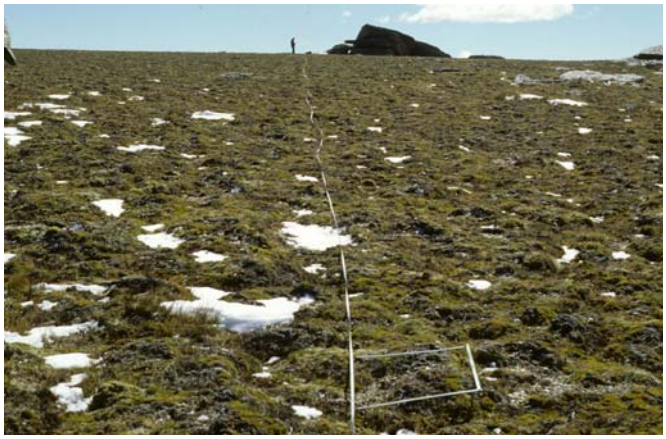
Appendix 2: List of common species in each TWINSPAN community.

Highly-modified	Tall-tussock	Short-tussock	Alpine
ACAagn	ANAbel	AIRcar	ABRinc
ACAbuc	GAUdep	ANTodo	ACAtes
AIRcar	DRAuni	BRAhaa	AGRmue
AREser	KELdie	CARbre	ANIfle
BROhor	DRApron	CARvex	CAREkir
BROtec	BLEpen	CELgrac	CARwak
CREcap	DRAace	CERfon	CELden
DACglo	LYCfas	COLstr	CELhaa
DICcri	CELspe	COPatr	CELlar
ECHvul	BRAbel	CREcap	CELses
ELYsol	GERmic	DICcri	CELvis
EROcic	ANIaro	DIStou	CHIden
GERses	ANIfle	ELYsol	CRAlan
MELalp	CELlya	FESnov	DRAmus
MYOdis	CHIsp	GERses	EUPzel
OXAexi		HELfil	GENbell
POAcit		HIElep	GERmic
POAman		HIEpil	GEUlei
POApra		HIEpra	GNAmac
RAOaus		HOLlan	HECcae
RAObea		HYDnov	KELdie
RAOpar		HYPrad	KOEshe
ROSrub		LEPpec	LUZpum
RUMace		LEUfra	LYCfas
RYTmac		LINcat	PLAlani
SPErub		LUZruf	POAcol
STEgrac		MICuni	POAton
TARoff		MUEaxi	RAOgra
TRIarv		POAcol	RAOhec
TRIdub		POAlin	RYTpum
TRIrep		RANfol	SCLuni
VERtha		RAOsub	TRIspi
VITaus		RUMace	UNCfus
VULbro		RYTpum	VIOcun
		STAmin	
		TRIarv	
		TRIrep	
		WAHalb	

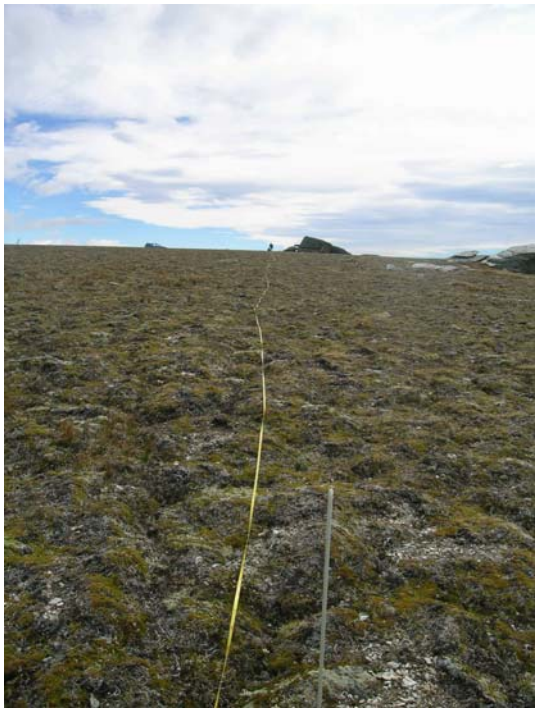
Appendix 3: Example photographs of each TWINSPAN community at each measurement.

Alpine native community with mat-forming species

First measurement



Second measurement



Third measurement

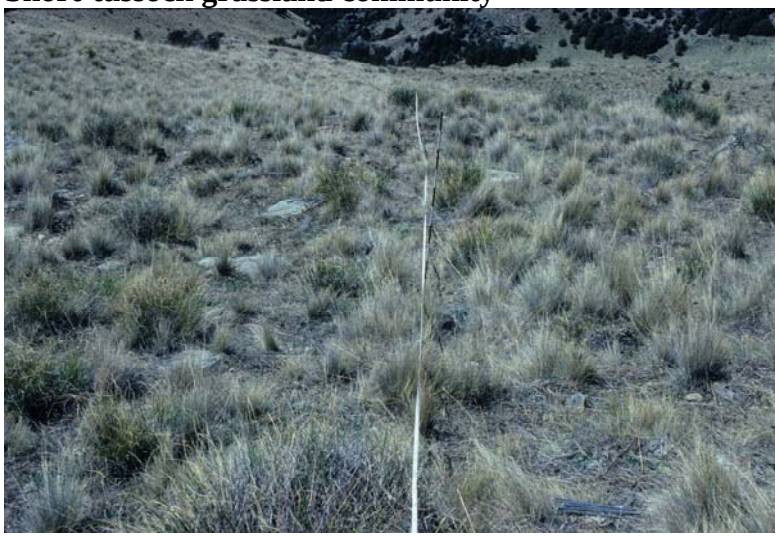
Tall-tussock grassland community

First measurement

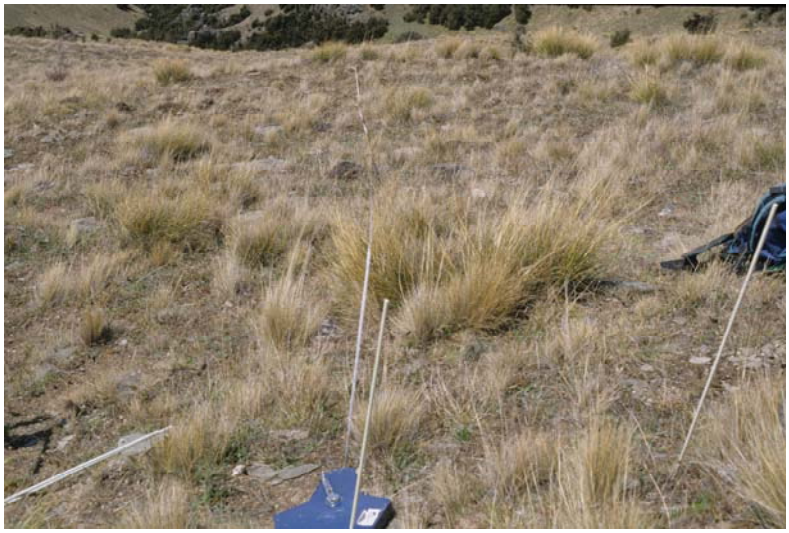
Second measurement

Third measurement

Short-tussock grassland community



First measurement



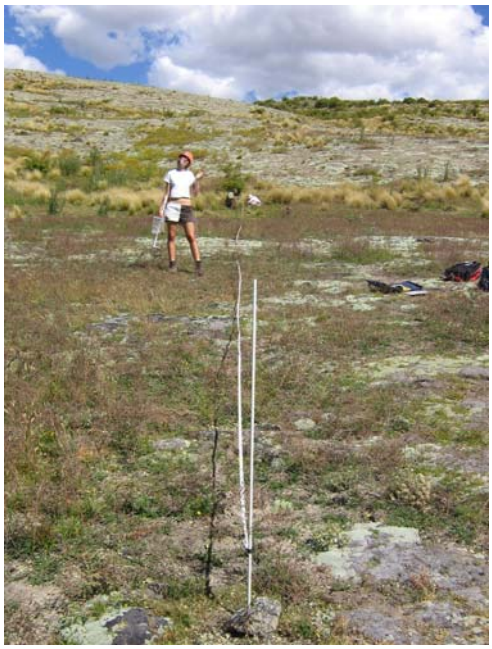
Second measurement

Third measurement

Highly-modified community

First measurement

Second measurement



Third measurement

Appendix 4: Transect information for transects under Department of Conservation tenure. Information for transects under pastoral tenure is not included to avoid the publication of information that identifies individual pastoral lease properties.

Site	Property	Tenure at first measurement	Tenure at second measurement	Tenure at third measurement	Easting	Northing	Status	Year officially transferred to DoC	Year of first measurement	Year of second measurement	Year of third measurement
FRAT001	Fraser Basin	PASTORAL	PASTORAL	DOC	2210300	5531500	DoC land Kopuwai Conservation Area	2002	1984	1998	2005
FRAT002	Fraser Basin	PASTORAL	PASTORAL	DOC	2207600	5535800	DoC Land - Lower Fraser Basin Special Lease	2002	1984	1998	2005
FRAT003	Fraser Basin	PASTORAL	PASTORAL	DOC	2207900	5538900	DoC Land - Lower Fraser Basin Special Lease	2002	1984	1998	2005
FRAT004	Fraser Basin	PASTORAL	PASTORAL	DOC	2207000	5540000	DoC Land - Lower Fraser Basin Special Lease	2002	1984	1998	2005
FRAT005	Fraser Basin	PASTORAL	PASTORAL	DOC	2205000	5539500	DoC Land - Lower Fraser Basin Special Lease	2002	1984	1998	2005
FRAT006	Fraser Basin	PASTORAL	PASTORAL	DOC	2203600	5538800	DoC Land - Lower Fraser Basin Special Lease	2002	1984	1998	2005
FRAT007	Fraser Basin	PASTORAL	PASTORAL	DOC	2206900	5536900	DoC Land - Lower Fraser Basin Special Lease	2002	1984	1998	2005
FRAT008	Fraser Basin	PASTORAL	PASTORAL	DOC	2212400	5539000	DoC land Kopuwai Conservation Area	2002	1984	1994	2005
FRAT009	Fraser Basin	PASTORAL	PASTORAL	DOC	2211200	5532800	DoC land Kopuwai Conservation Area	2002	1984	1998	2005
FRAT010	Fraser Basin	PASTORAL	PASTORAL	DOC	2210500	5534100	DoC land Kopuwai Conservation Area	2002	1984	1998	2005
KIRT020	Kirkliston	PASTORAL	DOC	DOC	2313400	5625400	DoC Stewardship Land	1987	1982	1995	2006
KIRT021	Kirkliston	PASTORAL	DOC	DOC	2314397.7	5624657.8	DoC Stewardship Land	1987	1982	1995	2006
KIRT024	Kirkliston	PASTORAL	DOC	DOC	2316399.3	5631056.3	DoC Stewardship Land	1987	1982	1995	2006

Site	Property	Tenure1	Tenure2	Tenure3	easting	northing	Status	Year officially transferred to DoC	First measurement	Second measurement	Third measurement
KIRT025	Kirkliston	PASTORAL	DOC	DOC	2316088.3	5630917.1	DoC Stewardship Land	1987	1982	1995	2006
KIRT026	Kirkliston	PASTORAL	DOC	DOC	2315873.3	5632036.9	DoC Stewardship Land	1987	1982	1995	2006
KIRT027	Kirkliston	PASTORAL	DOC	DOC	2315722.2	5631654.5	DoC Stewardship Land	1987	1982	1995	2006
OHAT010	Ohau Range	DOC	DOC	DOC	2251842.3	5654800	DoC Land	1981	1983	1997	2006
OHAT015	Ohau Range	DOC	DOC	DOC	2252056	5653561.9	DoC Land	1981	1983	1997	2006
OHAT019	Ohau Range	DOC	DOC	DOC	2251502.8	5652612.9	DoC Land	1981	1983	1997	2006
OHAT021	Ohau Range	DOC	DOC	DOC	2250208.3	5652141.8	DoC Land	1981	1983	1997	2006
OHAT024	Ohau Range	DOC	DOC	DOC	2250865.6	5651917.4	DoC Land	1981	1983	1997	2006
OHAT025	Ohau Range	DOC	DOC	DOC	2250421.7	5650978.2	DoC Land	1981	1983	1997	2006
OHAT042	Ohau Range	DOC	DOC	DOC	2255420.2	5651044.9	DoC Land	1981	1983	1993	2006
OHAT043	Ohau Range	DOC	DOC	DOC	2255124.2	5652116.5	DoC Land	1981	1983	1993	2006
OHAT044	Ohau Range	DOC	DOC	DOC	2255165.5	5656761.4	DoC Stewardship Land	1981	1983	1993	2006
OHAT045	Ohau Range	DOC	DOC	DOC	2255000.8	5657509	DoC Stewardship Land	1981	1983	1993	2006
PORT002	Porters	PASTORAL	DOC	DOC	2403473.2	5767309.4	DoC Land	1996	1984	1996	2006
PORT007	Porters	PASTORAL	DOC	DOC	2403543.5	5770115.9	DoC Land	1996	1984	1996	2006
PORT015	Porters	PASTORAL	DOC	DOC	2400443.5	5768718.8	DoC Stewardship Land	1987	1984	1996	2006
PORT016	Porters	PASTORAL	DOC	DOC	2400701.9	5768505.2	DoC Stewardship Land	1987	1984	1996	2006
STUT001	Mt Studholme	DOC	DOC	DOC	2344842.9	5614737.9	DoC Stewardship Land	1983	1983	1995	2006
STUT002	Mt Studholme	DOC	DOC	DOC	2344665.1	5615342.6	DoC Stewardship Land	1983	1983	1995	2006
STUT004	Mt Studholme	DOC	DOC	DOC	2344582	5614350.2	DoC Stewardship Land	1983	1983	1995	2006
STUT005	Mt Studholme	DOC	DOC	DOC	2344566.6	5614521	DoC Stewardship Land	1983	1983	1995	2006
STUT006	Mt Studholme	DOC	DOC	DOC	2344613.3	5614273.1	DoC Stewardship Land	1983	1983	1995	2006
STUT009	Mt Studholme	DOC	DOC	DOC	2344800	5615200	DoC Stewardship Land	1983	1983	1995	2006